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W. G. FARLOW

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JOHN MERLE COULTER

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ERRATA

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P. 53, line 4 from top, for UNIVERSITY OF OHIO read OHIO STATE UNIVERSITY
P. 57, line 12 from top, for fig. 4 read fig. 7
P. 65, line 4 from top, omit *(RPl)*
P. 109, line 12 from top, for average of 3 leaves read average indices of 3 leaves
P. 132, line 9 from top, for 61 read 60
P. 217, line 16 from top, for YAZIN read YASUI
P. 224, line 18 from top, for YAZIN read YASUI
P. 241, line 24 from top, for **Carya pallida** read **Carya pallida** Ashe
P. 246, line 9 from bottom, for southwestern read southeastern
P. 338, line 2 from top, for MOLTE read MALTE
P. 438, line 4 from bottom, for WOODHOUSE read WODEHOUSE

Volume LXVI Number 1

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JOHN M. COULTER

With the assistance of other members of the botanical staff of the
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VOLUME LXVI NUMBER 1

THE

BOTANICAL GAZETTE

JULY 1918

EXPERIMENTAL INVESTIGATIONS ON THE GENUS RAZOUMOFSKYA

JAMES R. WEIR

(WITH NINETEEN FIGURES)

Introduction

This article is the first of a series of reports on culture experiments of mistletoes. The work was begun in September 1911, and will be continued indefinitely. The aim of these experiments is to determine the validity of the several species as now distinguished, their affinities to each other, hosts on which they may be of economic importance or on which they may occasionally occur, and influence of host and condition of host as governed by its environment on the form, color, or other diagnostic characters commonly employed in the classification of these parasites. Since the systematic position and host relationships of several of these plants are not definitely defined, and since they are of great economic importance in many forest regions, it is believed the work will be of considerable value. The plan of these reports is to record as briefly as possible the results of each series of cultures as completed. The present report includes considerable discussion, owing to the necessity of outlining the problems in hand. The detailed discussion of results and technical description of species will be reserved until the conclusion of the experiments.

Methods

For that part of the work being conducted at Missoula, Montana, the opportunities are very favorable. Practically all the species of *Razoumofskya* of any economic importance are of easy access from the laboratory. Members of the field force of the United States Forest Service are aiding in the work by sending in fresh mature specimens of *R. pusilla* on spruce and larch from the Lake states, and of the rare unclassified forms occurring on white and yellow pines in Oregon, Idaho, Utah, and Nevada. A great deal of material of the common forms from all parts of the Northwest has also been contributed. The writer visits regularly the various forests of the Northwest and has made abundant collections of the mistletoes of these regions. The writer is under particular obligations to Professor W. C. WEIR for service in connection with cultures at Bellingham, Washington; to L. H. WEIR for collecting special material; to D. R. BREWSTER of the Forest Service Experiment Station, at Priest River, Idaho, and to J. DUNCAN, Superintendent of Parks of the city of Spokane, for permitting cultures to be made on various exotic conifers; and to E. E. HUBERT of this laboratory for assistance in making cultures.

From 1911 to 1914 inclusive the inoculations were conducted in the open. Seeds were sown on trial hosts of species other than that on which they developed, either in the same vicinity or in widely separate regions. In the latter case trial hosts of the same species as that on which the mistletoe grew were also included. This served to check the viability of the seed, also to bring out differences due to change of environment between the plants resulting from inoculation on the same host species and the plants furnishing the seed. The same was true for the plants on trial hosts other than that on which the parent plant developed. This double procedure demanded copious notes on the conditions of growth and general morphology of the plants furnishing the seed used in inoculations in other regions and the saving of specimens of both sexes for comparison afterward. The same was done with plants resulting from inoculation. In the latter case, where necessary, the infected branch or stem was cut out to prevent the spread of the parasite in new regions. A large number of specimens are accumulating, but this seemed desirable in case all necessary notes were not taken on both generations. In the case of continuing the inoculations of the same species of mistletoe through several generations on the same host but different individuals, either in the same or different localities, or on different host species, the saving of specimens fully recorded is doubly necessary. This should also furnish some information on the subject of the germinal transmission of characters.

Cultures begun in 1914 are being conducted both in the field and in the greenhouse. This doubles the amount of work, insuring greater dependency on results; and in the case of the indoor work closer study is possible of the life history of a successful inoculation. Indoor work also permits the use of a larger number of trial host species. The seeds germinate more rapidly and results are sooner obtained. One of the chief reasons for maintaining outdoor cultures is to check, whenever possible, under natural conditions, any unusual result obtained in the greenhouse. Cultures in the open have so far proved more successful than those inside, where the same mistletoes and hosts were concerned. If, however, a few unusual hosts are obtained indoors, it must be remembered that it is a new association of host and parasite often not possible in nature; moreover, some of the mistletoes showing the greatest predilection for a particular host or host genus are occasionally found on trees belonging to other genera.

In making the inoculations great care is exercised to attach the seeds at the most vulnerable points, such as in the axils of the leaf sheaths, tender branches, base of terminal buds, and in the denser zone of needles at the nodes. Observations show that infection usually occurs at these places.[1] Before the seeds are transferred to the host they are allowed to stand for a few minutes in water. This causes the mucilaginous coat of the seed to expand. The seeds are then sucked against the point of a dropping pipette and placed firmly in the desired position. After a short time the mucilaginous layer dries, holding the point of the seed in place.

The host material used in the inoculations ranges from seedlings 2 years old to the tender branches of mature forest trees. In case of the trial host possessing a suberized cortex the seeds are sown only on the first to the sixth year's growth. It has already been demonstrated that infection will not normally take place on older tissues.[3] It has been experimentally proven, however, that by scraping away the dead surface tissues of the bark on parts of branches as old as 7 years, and which still contain chlorophyll, it may be possible to secure infection. The number of seeds sown on each trial host has been maintained at 20 for greenhouse cultures and, owing to possible accident to the seed, 50 for outdoor work. It seemed desirable to try to maintain the seed at a fixed number so that the relative susceptibility of all trial hosts to any one form of mistletoe may be compared. Because it is impossible, especially of cultures in the open, to know that all seeds sown remained on the trees, the relative susceptibility of all trial hosts was further tested in most cases where it was particularly desirable to do so and whenever it was possible, by using a fixed number of trees of any one genus. A record of the source of seed of all trial hosts and of the place where the trees were grown was kept. This seemed desirable in view of the question of influence on the morphology of the parasite. In the case of transplants the trees had not been transplanted very long to the place where cultures were made. The seeds demand a period of rest before germination, and if stored under cool and moist conditions may be carried over and sown in the spring. Sowings as late as April have resulted in successful inoculations. The low temperatures of winter also seem beneficial to the seed, as it is observed that a higher percentage of seeds germinate which have undergone freezing temperatures. This probably accounts for the greater number of positive results obtained in outdoor cultures. If the seeds are stored in warm, dry air, they lose their vitality very rapidly, owing to the evaporation of moisture from the chlorophyllaceous endosperm. Germination tests show that the seeds are capable of germination some 2 weeks before they are normally expelled from the capsule, so that it has been possible to sow the seeds of some species early in September. Care must be taken in sowing seeds on *Larix* before

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[1] WEIR, JAMES R., *Wallrothiella Arceuthobii.* Jour. Agric. Research 4:377. 1915.

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[3] WEIR, J. R., Mistletoe injury to conifers in the Northwest. U.S. Dept. Agric. Bull. 360. p. 8. 1916.

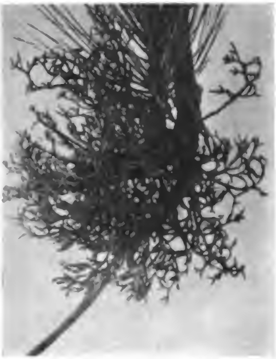

FIG. 1.—*Razoumofskya campylopoda* on *Pinus ponderosa:* slender, branching form with stems more or less cylindrical at base, pistillate; Oregon coast; reduced one-fourth.

the leaves have fallen; otherwise the seeds placed on the foliar spurs will be carried away with the falling leaves.

The cultures of the false mistletoes may be considered difficult. There must first be considerable knowledge of the requirements for seed germination, and of the plants afterward, in the case of the work done indoors. Much that is necessary has been learned, and the work is now going on more rapidly. The following is the first detailed report of the culture of mistletoes in this country. Some work of this kind but in another connection has already been reported by the writer (*loc. cit.*).

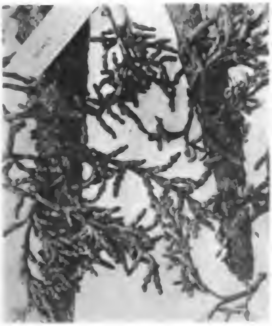

FIG. 2.—*R. campylopoda* on *Pinus ponderosa:* short, thick form with angular stems, staminate and pistillate plants; Oregon coast.

Cultures with yellow pine mistletoes

Razoumofskya campylopoda (Engelm.) Piper and *R. cryptopoda* (Engelm.) Coville, the largest and most conspicuous members of the genus in the United States, are supposedly 2 distinct species occurring on yellow pines. The former (figs. 1, 2, 6) is based on specimens from north Idaho or northeastern Washington, and is principally confined to the coast and northern Rocky

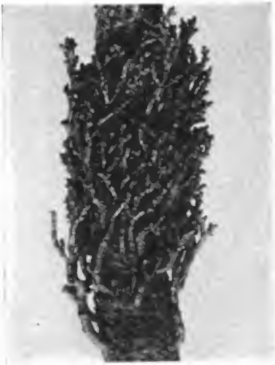

FIG. 3.—*R. cryptopoda* on *Pinus ponderosa:* pistillate; New Mexico; reduced one-fourth. —Photograph by G. G. HEDGCOCK.

Mountain regions.[3] The latter (figs. 3–5), based on specimens from New Mexico, is apparently limited to the southern Rocky Mountain regions. Both plants were originally described from specimens on *Pinus ponderosa*, which is their most common host. A large collection of these plants on *P. ponderosa* and a number of other hosts from their respective regions shows so few constant distinguishing characters by which the plants from the two geographical regions may readily be separated that it seemed desirable to test them out by cultures. Color, branching, thickness of stems, parting of flowers, and position of anthers on the calyx lobes, characters usually employed to distinguish one species from the other, are not always constant in these plants from the several regions in which they are supposed to occur, but apparently merge into one form or the other with change of habitat, just as is the case in any other species having a wide distribution and range of hosts. In a series of experiments recently completed by the writer and not otherwise mentioned in this paper it has

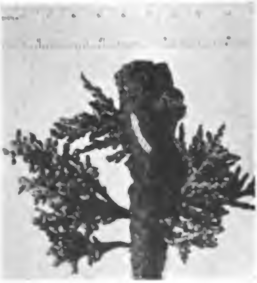

FIG. 4.—*R. cryptopoda* on *Pinus ponderosa:* staminate and pistillate; southern Utah.

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[3] PIPER, CHARLES V., Contrib. U.S. Nat. Herb. 11:222. 1906.

been demonstrated that size and color of flowers, stem, fruit, form and division of calyx lobes, slenderness and length of plant, compactness of individual colonies of the northern form depend upon age of the plants and of the infection, nourishment, condition, location, and species of host. In view of these results it seems desirable that the diagnostic characters as now employed in the separation of the large plants on yellow pines should be substantiated by a large number of cultures before they can be held specifically distinct. Experiments involving the transfer of seeds of the northern and coast plant from its various hosts to Rocky Mountain yellow pines, and vice versa, in their respective regions should be of some value in determining the validity of the two alleged species.

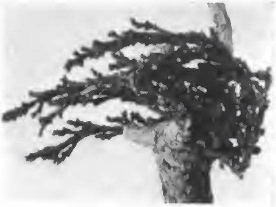

FIG. 5.—*R. cryptopoda* on *Pinus chihuahuana:* pistillate; reduced one-half.—Photograph by G. G. HEDGCOCK.

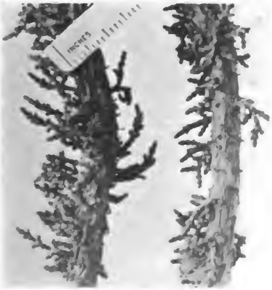

FIG. 6.—*R. campylopoda* on *Pinus ponderosa* as it often appears growing from an advancing cortical stroma in branches of witches' brooms: plants pistillate, mature.

R. occidentalis abietina Engelm. (figs. 7, 8) is a large form of mistletoe found on *Abies* throughout California, Washington, Oregon, and Idaho. It closely resembles the large mistletoes on yellow pines and is described as a variety of the form *R. campylopoda* (figs. 1, 2, 6) (*Arceuthobium occidentale*). The plant is not so large as the latter, but both have the same color variations and bloom and fruit in the same period. The facts that it is usually found in the same regions where the yellow pine mistletoe occurs, has the same diseases attacking it, and is not found in regions where the typical *R. tsugensis* is most abundant and which it also slightly resembles, indicate that it may be a biological form of the former. The results of a number of cultures involving the three plants mentioned are presented in table I.

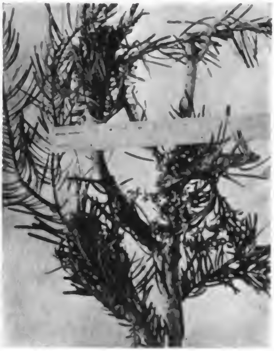

FIG. 7.—*R. occidentalis abietina* on *Abies concolor:* staminate and pistillate plants; Oregon.

It will be seen from table I that an effort has been made to sow the seed of the large mistletoes on *Pinus ponderosa* (figs. 1–6) from several localities on as many different hosts as possible and on the same host in widely separate regions. The object of the latter was to try to determine the relationship of the common mistletoes with thick, robust stems on yellow pine in the Rocky Mountain region to the more slender form on the same host in the Pacific Coast region. This problem has been sufficiently outlined previously. The cultures so far do not furnish any evidence that the two forms should be considered identical. Plants in the Pacific Coast region resulting from seed collected in the northern Rocky Mountain region, and vice versa, exhibit various color varia-

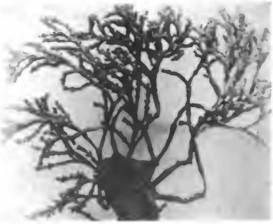

FIG. 8.—*R. occidentalis abietina* on *Abies nobilis:* staminate plants; Oregon.

tions, depending upon the region where grown. The same variation is noted in the robust form when grown in the North. This shows that these plants from the different localities cannot be held specifically distinct on a basis of color. Although color has been one of the chief distinctions between the two, the cultures show that there is no marked difference in the general morphology of each form when grown outside of its original place of collection. True, there are some differences to be noted with respect to size, but it is purely a matter of age of infection. Even after the first maturity these plants, which have a comparatively long life, grow larger by developing additional branches and increasing the thickness of the stem. The comparisons made in the table are based on plants differing widely in age; consequently measurements must vary slightly. Excepting color changes, which were to be expected from varying habitats, the general morphology of the younger plants of the parent colonies were in no particular different from those of the cultures. The cultures have also demonstrated the fact that *R. campylopoda* will infect *Abies*, with considerable variation in color and size of the resultant plants, but closely resembling the form known as *R. occidentalis abietina*. It is interesting to note in this connection that COVILLE[4] refers the plant found on *Abies magnifica* and *A. concolor* directly to *R. campylopoda* (*R. occidentalis* [Engelm.] Coville) with the statement that it is probably the plant that ENGELMANN[5] had previously described under this name (*Arceuthobium campylopodum*). It is further shown that *R. campylopoda* will infect *Picea* and *Larix*, but with difficulty.

This mistletoe also will apparently readily infect *Pinus contorta*, a result repeatedly confirmed in the field. This tree, however, is not a common host. As will be shown in the case of *R. americana*, it is believed that this parasite may be expected to occur on any hard or yellow pine, but with predilection for certain species. The mere assumption that hosts are the determining factors of a species is here shown to be untenable. When a parasitic species will infect hosts from widely separate regions and even genera, and the resulting plants have certain characters varying from those exhibited

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[4] Contrib. U.S. Nat. Herb. **4**:192. 1893.

[5] GRAY, ASA, Pl. Lindh. **2**:214. 1850.

TABLE I

SEED COLLECTED SEPTEMBER 25, 1911, ST. MARIES, IDAHO; SEPTEMBER 29, 1912, SANTA BARBARA NATIONAL FOREST, CALIFORNIA; SEPTEMBER 30, 1912, AND AT INTERVALS FROM SEPTEMBER 4 TO NOVEMBER 14, 1914, AT SPOKANE, WASHINGTON, AND IN UTAH, FROM THE LARGE MISTLETOES ON *Pinus ponderosa* COMMONLY KNOWN IN THEIR RESPECTIVE REGIONS AS *R. campylopoda* AND *R. cryptopoda;* CULTURES FROM SEED COLLECTED IN THE SANTA BARBARA NATIONAL FOREST, CALIFORNIA, MARKED *A;* CULTURES FROM SEED COLLECTED AT ST. MARIES, IDAHO, MARKED *B;* CULTURES FROM SEED COLLECTED IN UTAH MARKED *C.*

TRIAL HOSTS			LOCALITY WHERE CULTURES WERE MADE AND DATE	RESULTS OF CULTURES	
Name and number used in cultures	Source of seed	Locality grown		Date of first observation of germination	Results (measurements averaged)
Pinus ponderosa (2)......	Local	Local	Priest River, Idaho 10–6–12, *A**	6–26–13	October 14, 1916: 1 infection on each host; all staminate (*a*) 3 cm. high, deep olive,‡ mature, flowering spikes 1 cm. long (no. 637); (*b*) 3 cm. high; general color, yellowish olive; nodes vinaceous brown (no. 638); parent, 6 cm. high; much branched, yellowish olive (no. 636).
Pinus ponderosa (2)......	Local	Local	Priest River, Idaho 10–4–12, *C**	5–10–13	October 15, 1916: 1 infection on each host, staminate and pistillate; former 3.5 cm. high, robust, thick at base; branches, somewhat paniculate, dark greenish olive; floral spikes 1 cm. long; flowers mostly 3-parted, compressed; latter 5 cm. high, stems thick at base, light brownish olive, mature; seed greenish olive, 3.02 by 1.44 mm.; parent, pistillate; stems light olive yellow, thick at base, robust throughout, 4 cm. high; fruit, olive yellow; seed, 3.04 by 1.45 mm.; staminate, olive yellow; branches, short, 4 cm. high; floral spikes, 1.5 cm. long; flowers, 3 and 4-parted.

Pinus ponderosa (2)......	Cal.	Cal. and Wash.	Bellingham, Wash. 10–10–11,* *B*	4–10–12	September 19, 1915: 3 infections: (*a*) staminate, (*b*) staminate, (*c*) pistillate; all 5 cm. high. (*a*) Stems seal brown; floral spikes, light yellowish olive mature; 1 cm. long; flowers mostly 3-parted; exposed (no. 671). (*b*) Stems uniformly olive yellow; floral spikes 7 mm. long; flowers 3 and 4-parted; developed in shade (no. 672). (*c*) Olive yellow; fruiting spike darker; fruit vinaceous gray; seed 3.02 by 1.45 mm. (no. 673). Parent, pistillate, 6 cm. high; stems tawny olive; fruit pale green-blue gray; seed 3.0 by 1.3 mm. (no. 674); staminate§ 9 cm. high, dark greenish olive; floral spikes 2 cm. long; mostly 4-parted (no 675).
Pinus ponderosa (2)......	Local	Local	Missoula, Mont. 10–25–12*	5–10–13	October 1, 1916: 1 infection; pistillate, 6 cm. high, branched, uniformly light brownish olive; fruit not produced (no. 639); parent 5 cm. high, uniformly dark livid brown (no. 640).
Pinus ponderosa (var. scopulorum) (2)......	S.D.	Mont.	Priest River, Idaho, (Experiment Station) 10–4–12,* *A*	6–19–13	October 15, 1916: 1 infection; pistillate, 2 cm. high, light yellowish olive (no. 641); parent yellowish olive (no. 635).
Pinus ponderosa (2)......	Colo.	Colo.	Priest River, Idaho (Experiment Station) 10–4–12,* *A*	6–19–13	October 15, 1916: 1 infection on each host, staminate and pistillate; former 3 cm. high, light olive, yellow floral spikes 1.5 cm., flowers mostly 3-parted (no. 632); latter 2.5 cm. high, yellowish olive, mature, seed 3.02 by 1.42 mm. (no. 631); parent pistillate; stems isabel, fruit russian blue, seed 3.1 by 1.53 mm. (no. 633); staminate, light brownish olive, much branched, 7 cm. high, floral spikes 2 cm. long, flowers 3 and 4-parted (no. 634).

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* Cultures in field.

‡ All color names taken from Ridgway's color standards and nomenclature.

§ Nearest to pistillate plants from which seeds were used.

TABLE I—*Continued*

TRIAL HOSTS			LOCALITY WHERE CULTURES WERE MADE AND DATE	RESULTS OF CULTURES	
Name and number used in cultures	Source of seed	Locality grown		Date of first observation of germination	Results (measurements averaged)
Pinus ponderosa (2)......	Cal.	Ore.	Priest River, Idaho (Experiment Station) 10-4-12*	6-19-13	October 15, 1916: 1 infection, pistillate, 2 cm. high, ecru-olive (no. 642); parent olive yellow, fruit russian blue (no. 643).
Pinus ponderosa (2)......	Local	Local	Priest River, Idaho 10-6-12,* *A*	6-26-13	October 14, 1916: 1 infection, pistillate, 3 cm. high, buffy olive (no. 644); parent 8 cm. high, clay color (no. 645).
Pinus ponderosa (2)......	N.M.	Mont.	Missoula, Mont. 10-10-14*	4-28-15	November 1, 1916: 1 infection, plants appearing; tree died on being transplanted into greenhouse.
Pinus contorta (2).......	Local	Local	Priest River, Idaho 10-6-12,* *A*	6-26-13	October 14, 1916: 1 infection, staminate, 4 cm. high, dark greenish olive, floral spikes 1.5 cm. long, flowers 3 and 4-parted (no. 647); parent pistillate, 7 cm. high, olive-ocher, fruit yellowish olive (no. 648); staminate, 5 cm. high, honey yellow flowered, spikes 1 cm. long, flowers mostly 3-parted.
Pinus contorta (2).......	Local	Local	Priest River, Idaho 10-6-12*	6-26-12	October 14, 1916: 2 infections on 2 different trees; plants pistillate, one 3.5 cm. high, purplish lilac at nodes, remainder of stem reed yellow, fruit not produced (no. 629); the other (no. 630) 2 cm. high, yellowish olive, fruit not produced; parent honey yellow, on same branch with deep yellow staminate plants (no. 628).
Pinus Jeffreyi (2)........	Cal.	Cal.	Missoula, Mont. 12-22-14†	2-16-15	January 3, 1917: 2 infections; plants staminate, 3 cm. high, olive yellow (no. 646); parent yellowish olive (no. 649).
Pinus resinosa (2)	Minn.	Idaho	Priest River, Idaho (Experiment Station) 10-4-12,* *A*	6-19-13	October 15, 1916: 1 infection, staminate, infected twig stunted, almost dead; one plant attached, remainder fallen, army brown (no. 650); parent light yellowish olive, fruit dark greenish olive (no. 651).

Pinus sylvestris (2)........	Europe	Spokane	Spokane, Wash. 11-10-11*	....	December 14, 1916: 3 infections, 2 on one stem 2 cm. apart, 1 staminate, 1 pistillate; former 4 cm. high, stems vinaceous drab, floral spikes wax yellow, mature (no. 623); latter 2.5 cm. high, light yellowish olive (no. 623); third infection plant, pistillate, 5 cm. high, not uniformly yellowish olive, internodes purplish gray, fruit not produced (no. 624); parent uniformly yellowish olive, 4 cm. high (no. 625).
Pinus montana (2)........	Europe	Spokane	Spokane, Wash. 11-10-11*	....	December 14, 1916: 1 on each host, both pistillate, 1 stunted, 4 mm. high, olive yellow (no. 626); other 3.5 cm. high, vigorous, light yellowish olive (no. 626); parent pistillate, 6 cm. high, honey yellow, fruit light drab; staminate stems on same branch, dark greenish olive, floral spikes yellowish olive (no. 627).
Larix occidentalis (4).....	Idaho	Idaho	Priest River, Idaho 10-6-12*	6-26-13	October 14, 1916: 1 infection, plants staminate, 3 cm. high, greenish yellow, had flowered, parent staminate, plain yellow (no. 684).
Larix occidentalis (4).....	Mont.	Mont.	Missoula, Mont. 12-22-14†	2-16-15	May 1, 1916: Penetration of sinker; no further result.
Larix europea (4)........	Europe	Idaho	Missoula, Mont. 10-14-14†	2-16-15	May 1, 1916: Penetration of sinker; no further result
Picea excelsea (1)........	Europe	Idaho	Missoula, Mont. 10-21-14†	2-26-13	November 1, 1916: 1 infection; pronounced fusiform swelling of branch, plants small, barely protruding, 1 mm. in diameter.
Abies grandis (2).........	Local	Local	Priest River, Idaho 10-6-12*	6-26-13	October 14, 1916: 1 infection, pistillate plants 3 cm. high, honey yellow (no. 652); parent (no. 643).
Abies concolor (2)........	Ore.	Cal.	Spokane, Wash. 11-10-11,* *B*	....	October 13, 1916: 2 infections; staminate plants 4 cm. high, mature, dark greenish olive (no. 653); pistillate, 3 cm. high, dark greenish olive (no. 654); parent (no. 643).

* Cultures in field. † Greenhouse. ‡ All color names taken from Ridgway's color standards and nomenclature.

by the parent when growing on what we may term the mother host, the limitations of a species are naturally more difficult to define. Notwithstanding this change, however, a good species should be sufficiently characteristic on any host and under any of the ordinary conditions of growth as to be readily recognized by one having a wide knowledge of the plant in the field. We do not think of the low, scrubby Douglas fir of central Montana as anything different from the gigantic form of this tree occurring in the Puget Sound region.

It is of considerable economic importance that *R. campylopoda* will infect *Pinus resinosa*, *P. sylvestris*, and *P. montana*, and may be expected to be a serious pest on these trees in localities where conditions are favorable. In drier sites of the Lake states and, in fact, throughout the Northeast, where it is proposed to plant *P. resinosa*, this mistletoe would undoubtedly grow luxuriantly. and care should be exercised against its introduction into these regions on nursery stock during the early period of infection.

Seeds of *R. campylopoda* were sown on the following pines in most cases in the greenhouse, but either due to the poor quality of the seed, loss of seed, or low vigor of the trial hosts the results were mostly negative. This does not mean, however, that all of the species mentioned here are immune. In a few cases infection did occur on species not mentioned in the table, but the results were of a nature that it is thought best not to report them at this time. These were *Pinus Banksiana*, *P. mayriana*, *P. Strobus*, *P. Cembra*, *P. cembroides*, *P. edulis*, *P. Lambertiana*, and *P. monticola*. Sowings made on *Pseudotsuga taxifolia*, *Larix leptolepis*, *Tsuga heterophylla*, *Thuja plicata*, *T. occidentalis*, *Cupressus arizonica*, *Picea Engelmanni*, *P. canadensis*, *Populus tremuloides*, *P. trichocarpa*, *Betula occidentalis*, *Alnus tenuifolia*, *Acer glabrum*, and *Prunus demissa* resulted negatively.

SUMMARY.—Results of cultures so far indicate that the mistletoes known under the names *Razoumofskya campylopoda* and *R. cryptopoda* are distinct. Each form, however, may exhibit considerable variation, due to geographic location and host. The relationship of the two forms will be further considered when a number of experiments now being conducted are completed.

Cultures show that the plant known as *R. occidentalis abietina* on *Abies* is in all probability a biological form of *R. campylopoda*. The taxonomic position of the plant, however, cannot be established with any certainty until it is successfully grown on yellow pine.

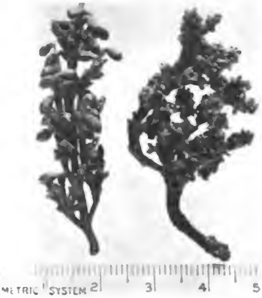

FIG. 9.—*R. laricis* on *Larix occidentalis:* staminate and pistillate plants.

Cultures with larch mistletoe

From the fact that this parasite, *R. laricis* Piper (figs. 9, 10), exhibits considerable variation under different conditions of growth and will occasionally grow on other hosts than *Larix*, it seemed desirable to study the species in culture. The chief results of these experiments are embodied in table II. These results indicate that *Larix* is the true host genus for *R. laricis*. The fact that 6 trees of *Larix occidentalis* were infected out of 6 on which seed were sown demonstrated the close affinity of the host and parasite. The readiness with which *R. laricis* infects *Larix europea* and *L. leptolepis*, the common Japanese larch, shows that this parasite may be expected to cause serious injury to plantations of these species not only in America, but in many parts of Europe and Japan as well, wherever climatic conditions are

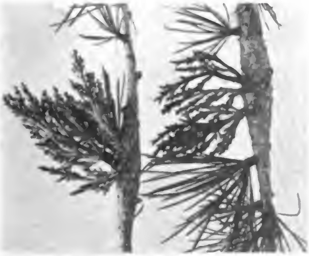

FIG. 10.—*R. laricis* on *Larix occidentalis:* pistillate plants; reduced one-half.

TABLE II

SEED COLLECTED AT ST. MARIES, IDAHO, SEPTEMBER 24, 1911; PRIEST RIVER, IDAHO, SEPTEMBER 20 AND 30, 1912; FROM *R. laricis* ON *Larix occidentalis;* ALL CULTURES MADE IN THE FIELD.

TRIAL HOSTS			LOCALITY WHERE CULTURES WERE MADE AND DATE	RESULTS OF CULTURES	
Name and number used in cultures	Source of seed	Locality grown		Date of first observation of germination	Results (measurements averaged)
Larix occidentalis (2).....	Local	Local	Coeur d'Alene, Idaho 11-5-11	....	August 25, 1915: 2 infections; plants staminate, 2.5 cm. high; flowers reed yellow, 3 and 4-parted, stems olive yellow; parent lime green, upper half of fruit purplish lilac.
Larix occidentalis (2).....	Local	Local	Blue Lake, Idaho 10-3-12	6-18-13	October 14, 1916: 2 infections on one host; plants pistillate, 4 cm. high, stems dark livid purple; spikes olive yellow developed in direct light; parent uniformly light yellowish olive, grew in diffused light.
Larix occidentalis (2).....	Local	Local	Missoula, Mont. 10-30-12	6-6-13	September 8, 1915: 2 infections, pistillate, 4.5 cm. high, stems olive ocher, fruit lime green, culture in dense shade; parent dark olive buff, fruit with pale bluish lavender points, growing in strong light.
Larix europea (2)........	Europe	Wash.	Spokane, Wash. 11-11-11	....	October 13, 1916: 3 infections, 1 staminate, 2 pistillate; former 3 cm. high, dark vinaceous brown, mature in 1914, flowers lime green, flowers mostly 3-parted (no. 658); latter 2 cm. high, joints dark vinaceous brown, fruit dark greenish olive (nos. 656 and 657); parent; pistillate stems dark livid brown, fruit light yellowish olive (no. 659); staminate stems on same branch, olive yellow flowers, mostly 4-parted (no. 685).

Larix leptolepis (2).......	Japan	Idaho	Priest River, Idaho 10–4–12	6–19–13	October 15, 1916: 1 infection, pistillate, 2 cm. high, stems light yellowish olive, fruit with bluish tips (no. 654); parent dark livid purple (no. 655)
Pinus ponderosa (6)......	Local	Local	Coeur d'Alene, Idaho 11–7–11	....	August 25, 1915: 1 infection, plants pistillate, 4 cm. high, dark greenish olive, vigorous at time of collection (no. 662); parent honey yellow (no. 663).
Pinus contorta (6).......	Local	Local	Blue Lake, Idaho 10–6–12	6–18–13	October 14, 1916: 1 infection, staminate, 3 cm. high, stems yellowish olive, joints dark vinaceous drab, flowers distantly alternate-opposite, mostly 3-parted (no. 660); parent; pistillate, stems dark vinaceous brown, fruit light yellowish olive (no. 661); staminate, stems on same host anthracene purple, flowers mostly 4-parted, closely alternate-opposite.
Abies grandis (6)........	Local	Local	Blue Lake, Idaho 10–2–12	6–18–13	October 14, 1916: 1 infection; staminate, apparently vigorous for a time, but at this date plants were dead and mostly fallen; original color not determined with certainty but appeared purplish (no. 664); parents light yellowish olive with darker colored fruit (no. 665).

favorable. The nature of the results on *Pinus ponderosa* and *P. contorta*, although demonstrating that this mistletoe under very favorable conditions will infect yellow pines, does not show any great affinity for the genus. When it is recalled that 900 seeds were sown on 18 individuals of *Pinus ponderosa*, each receiving 50 seeds, resulting in one infection, and one infection on *P. contorta* out of 12 trees tested with 600 seeds, the relationship between these 2 tree species and the larch mistletoe cannot be very close. The same is apparently true with regard to the infection of *Abies grandis*. Six trees were tested with the usual number of seeds, but only 1 infection resulted, which later died. These cultures also show that seeds germinating in the most vulnerable places only cause infection. Out of 500 seeds sown on *Larix* only 10 were able to cause infection, although apparently all the seeds which remained on the trees germinated. All were sown on parts of branches or shoots not over 6 years old, and care was taken to place the seeds favorably. It is to be expected that some of the seeds in outdoor cultures are removed by wind, rain, snow, insects, or birds. The observations relative to the favorableness of seed placement do not apply in the same way to the cultures on *Pinus* and *Abies*, since the larch mistletoe does not exhibit any marked affinity for these genera. That the same species of mistletoe growing on different hosts or under different conditions on the same host may exhibit different morphological characters is clearly demonstrated by these cultures.

Since these experiments with the larch mistletoe were started, the following field observations have been made near Fernan Lake, Idaho. A large veteran western larch severely infected with *R. laricis* was left standing in a clearing which reseeded to *Pinus ponderosa* and *P. contorta*. From one each of these species growing directly under the larch typical, although small, specimens of the larch mistletoe bearing both pistillate and staminate plants were collected. The only true pine mistletoe in the immediate vicinity was *R. americana*. In a canyon near Missoula, Montana, where the larch is seriously infected with *R. laricis* and the pine mistletoes are not known to occur, specimens of the former have been collected from a single infection on *Pinus contorta*. These results are very much at variance with previous ideas of the host affinities of *R. laricis*, but they should not alter in the least the economic situation, since infections very rarely occur. The fact that both pines and larches are resinous may explain the occasional occurrence of the parasite on the former hosts. Although great pains were taken to place the seed in favorable places on the trial hosts, the results on the following species were negative: *Pseudotsuga taxifolia*, *Pinus monticola*, *Picea Engelmanni*, *Thuja plicata*, *Tsuga heterophylla*, *Taxus brevifolia*, *Juniperus communis*, *Populus tremuloides*, *P. trichocarpa*, *Betula occidentalis*, *Alnus tenuifolia*, and *Salix Bebbiana*. Field observations on the intermingling of the branches of most of these species with severely infected branches of larch-bearing pistillate plants confirm the results of the cultures. Such observations, however, cannot be used as conclusive evidence for determining the host range for any one species of mistletoe.

SUMMARY.—The hosts of *Razoumofskya laricis* are *Larix occidentalis*, *L. Lyalli*, *L. europea*, *L. leptolepis*, *Abies grandis*, *Pinus ponderosa*, and *P. contorta*. The parasite is known to be of economic importance to the first named species only. The plant resulting from an infection on any other host than that on which it normally grows exhibits considerable change in morphology and also in vigor. That different degrees of exposure with respect to light very greatly influence the color of the plants is very clearly demonstrated.

Cultures with Razoumofskya species having purple flowers

A group of small mistletoes found in the western United States has one character in common with *R. pusilla* of the East, namely, deep purple flowers.[6] They are *R. Douglasii abietina* (Engelm.) Piper[7] on *Abies* (figs. 11, 12), *R. Douglasii* (Engelm.) Kuntze on *Pseudotsuga* (fig. 15), and a small form on *Picea* (figs. 13, 14). A careful comparison of representative collections of these 3 plants from varied environments shows no constant characters by which they may be held as distinct species. All three have 2, 3, or rarely

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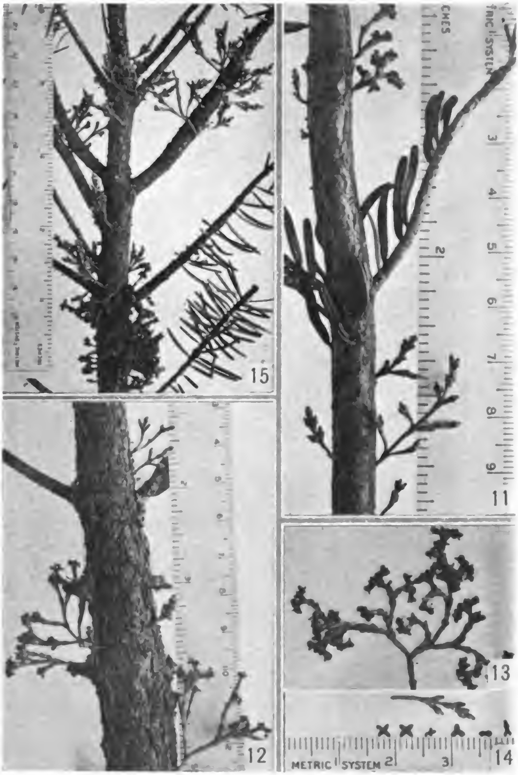
[6] WEIR, J. R., *Wallrothiella Arceuthobii*. Jour. Agric. Research 4:372. 1915.

[7] Reported by ENGELMANN under the name *Arceuthobium Douglasii* var. *abietinum* in S. Watson, Bot. Cal. 2:106. 1880.



FIGS. 11–15.—Fig. 11, *R. Douglasii* on *Abies grandis*, staminate and pistillate plants; fig. 12, *R. Douglasii* on *Abies lasiocarpa*, staminate and pistillate plants; fig. 13, small purple-flowered form on *Picea Engelmanni*, staminate plant, natural size; fig. 14, small purple-flowered form on *Picea Engelmanni*, staminate flowers and pistillate plant; fig. 15, *R. Douglasii* on *Pseudotsuga taxifolia*, staminate and pistillate plants.

4-parted purple flowers, solitary or clustered, simple or branched, according to age of infection, bloom and fruit in the same season; and size of fruit, flower, plant, and color of stems show some variations under different conditions of growth. Cross inoculations involving these forms should demonstrate whether or not all 3 are identical with *R. Douglasii*. The results of a series of cultures are given in tables III and IV.

At the time these cultures with *R. Douglasii* and *R. Douglasii abietina* were made seeds of the form on *Picea* were not available. The plant is not morphologically different from the other two, and cultures now under way indicate that it will infect *Abies* and *Pseudotsuga*. The evidence so far obtained is so pointedly in favor of the view that all 3 forms are identical that there can be little room for doubt. We find, for instance, that *R. Douglasii* will infect *Abies grandis*, *A. lasiocarpa*, and *A. concolor*, which are hosts for *R. Douglasii abietina*. No marked morphological differences are found in the resultant plants and their parents, any more than is to be expected from a change of host or condition of growth. The same is true for the culture of this mistletoe on *Picea Engelmanni*. The evidence that all 3 forms are identical is further strengthened by the fact that *R. Douglasii abietina* from *Abies lasiocarpa* will infect *Pseudotsuga laxifolia* and *Abies grandis*, and that it is possible to fertilize the pistillate flowers of this form on the latter host with pollen from plants on *Pseudotsuga*. These results demonstrate the relationship of the 3 small purple-flowered forms here considered. The two forms on *Abies* and *Picea* should be considered identical with *R. Douglasii* in view of the foregoing results. It has already been pointed out that, in the writer's experience, the plants on *Abies* and *Picea* are in most cases found in localities where *R. Douglasii* abounds. If the former were specifically distinct, with inherent tendencies to select their particular hosts, they should in the light of our knowledge of the well defined species be more abundant. On the contrary, they are never found in any quantity. The conclusion that *R. Douglasii* does not abundantly infect other trees than Douglas fir is also shown by the following observations. The writer has looked several times in vain for infection of this species on *Abies* and *Picea* when the

TABLE III

SEED COLLECTED OCTOBER 28, 1911, SEPTEMBER 20, 1912, AND OCTOBER 1, 1914, AT MISSOULA, MONTANA, FROM *R. Douglasii* ON *Pseudotsuga taxifolia*.

TRIAL HOSTS			LOCALITY WHERE TESTS WERE MADE AND DATE	RESULTS OF CULTURES	
Name and number used in cultures	Source of seed	Locality grown		Date of first observation of germination	Results (measurements averaged)
Pseudotsuga taxifolia (2)..	....	....	Priest River, Idaho 10–5–12*	6–17–13	April 14, 1916: 1 infection; staminate, 1.5 cm. high, solitary, dark olive gray, flowers blackish purple; parent, light yellowish olive with lighter colored flowers; former in direct light, latter in shade.
Abies lasiocarpa (2)......	Mont.	Mont.	Missoula, Mont. 10–24–14†	2–8–15	Pronounced swelling at several points; apparent infections; plants never appeared.
Abies grandis (2)........	Mont.	Mont.	Missoula, Mont. 10–24–14†	2–6–15	One infection but died out; host in poor condition.
Abies grandis (2)........	....	....	Priest River, Idaho 10–5–12*	6–17–13	October 14, 1916: 1 infection; pistillate, plants 2 cm. high, simple, solitary, light yellowish olive, fruit dark greenish olive, mature, flowers fertilized from plants resulting from inoculation on *Pseudotsuga* which were 2 m. distant, seed were immediately sown on *Pseudotsuga;* parent brownish, 3 cm. high, were deep olive gray with slightly lighter colored fruit.
Abies concolor (2).......	....	....	Spokane, Wash. 11–10–11*	....	April 14, 1916: 1 infection, staminate, 2 cm. high, solitary, slender, light yellowish olive, flowers vernonia purple, 2 and 3-parted, in shade (no. 670); parent, 3 cm. high, clustered, branched, yellowish olive, with purplish fruit, grew in direct light; staminate, 2.5 cm. high, clustered, branched, rather thick for species, olive buff, flowers vernonia purple, 3-parted, grew in shade.
Picea Engelmanni (2)	....	....	Priest River, Idaho 10–5–12*	6–17–13	April 14, 1916: 1 infection; staminate, 2.5 cm. high, solitary, branched, flowers vernonia purple, plants light yellowish olive (no. 676); parent, pistillate, 3 cm. high, simple, solitary, dark olive gray with purplish tipped fruits (no. 677); staminate, 3 cm. high, clustered, simple, flowers dark corinthian purple.

* Cultures in field. † Greenhouse.

TABLE IV

SEED COLLECTED ON BALD MOUNTAIN NEAR LAKE PEND OREILLE OCTOBER 2, 1912, FROM *R. Douglasii abietina* ON *Abies lasiocarpa*.

TRIAL HOSTS			LOCALITY AND DATE	RESULTS OF CULTURES	
Name and number used in cultures	Source of seed	Locality grown		Date of first observation of germination	Results (measurements averaged)
Pseudotsuga taxifolia (4)..	Local	Local	Priest River, Idaho 10–6–12	6–17–13	April 14, 1916: 1 infection; staminate, 2 cm. high, solitary, branched, light yellowish olive, flowers blackish purple (no. 678); parent (no. 679), not differing in any particular feature with the exception of staminate flowers of parent plants were slightly larger and of a lighter color.
Pseudotsuga taxifolia (4)..	Local	Local	Blue Lake, Idaho 10–9–12	6–18–13	April 14, 1916: 1 apparent infection, swelling of branch; plant did not appear.
Abies grandis (4)........	Local	Local	Priest River, Idaho 10–8–12	6–17–13	October 14, 1916: 1 infection; pistillate, solitary, branched, 3 cm. high, light yellowish olive, fruit mature, artificial pollination from no. 678, brownish purple at tips, seed immediately sown on *Pseudotsuga*; parent, 3.5 cm. high, simple, solitary, dark olive-gray, fruit dark greenish olive (no. 681).

latter grew in absolute contact with brooms on Douglas fir bearing pistillate plants. As previously stated, however, this is not conclusive evidence of the host range of a species. Accident of infection is too great; besides, trees growing in such juxtaposition are very often suppressed, thus reducing the amount of vulnerable tissue. These results were obtained only by the most careful placing of the seeds at the most susceptible points. In the course of years such conditions occur in nature. Afterward, as a matter of course, further infection from the parent tree to others of its kind may be easier. The type of broom produced by *R. Douglasii* varies with age and host. On hosts with strongly excurrent growth, such as *Abies lasiocarpa* and *A. grandis*, the brooms are usually erect, but drooping or swaying forms occur. The erect type of broom is common on *Pseudotsuga taxifolia* during the first years of infection, but later may assume the weeping willow form.

Seeds from plants on *Abies lasiocarpa* were sown on a single individual each of *Tsuga heterophylla*, *Larix occidentalis*, *Pinus monticola*, *Thuja plicata*, and *Populus trichocarpa*, but without results. Seeds from plants on *Pseudotsuga taxifolia* were without result on these hosts and also on *Larix europea*, *Picea sitchensis*, *P. canadensis*, *P. excelsea*, *P. Parryana*, *Sequoia gigantea*, *Pinus ponderosa*, *P. contorta*, *P. Jeffreyi*, *P. sylvestris*, *Betula occidentalis*, *Alnus tenuifolia*, and *Pyrus*. The several species of *Picea* were not in a vigorous condition, having been transplanted only a short time before the seed were sown.

SUMMARY.—The foregoing cultures indicate that *Razoumofskya Douglasii abietina* is identical with *R. Douglasii*. The hosts of *R. Douglasii* as known to the writer are *Pseudotsuga taxifolia*, *Picea Engelmanni*, *Abies concolor*, *A. grandis*, *A. lasiocarpa*, *A. nobilis*, and *A. amabilis*. The species is of economic importance only on *Pseudotsuga taxifolia*.

Cultures with lodgepole pine mistletoe

This species (*R. americana* [Nutt.] Kuntze) (figs. 16, 17) is one of the most characteristic of the genus. In order to determine its host range, the results of some recent cultures are presented in table V. It is shown that *Pinus contorta* is the true host of *R.*

americana, but that occasionally other hard pines are attacked. The writer has previously reported the occurrence of this mistletoe on *Pinus attenuata*, *P. Jeffreyi*, and *P. ponderosa*, and it has long been known to be common on *Pinus Banksiana* in Canada. The fact that this mistletoe will infect *Pinus montana*, the common mountain pine of Europe, further supports the writer's contention that it may be expected to occur occasionally on any of the hard or yellow pines, and also is a warning that the parasite would probably find a favorable home in Europe. The plant apparently attacks the yellow pines other than *Pinus contorta* with difficulty. Such infections are by no means common, and frequently result in some morphological changes in the plant. These changes, however, may not be any more marked than those the plant may exhibit when developing under various light intensities or varying conditions of nourishment on its regular host. If *R. americana* exhibits a certain antipathy to other yellow pines, it apparently has a much greater aversion to white pine. That the species will infect white pines but with difficulty, and will never be of consequence in this respect, is shown by the discovery of two infections on *Pinus albicaulis* near Darby,

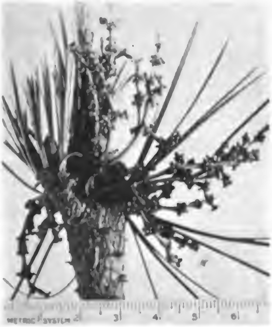


FIG. 16.—*R. americana* on *Pinus ponderosa:* staminate plants.

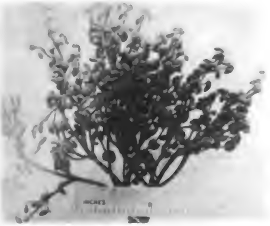


FIG. 17.—*R. americana* on *Pinus contorta:* pistillate plants.

TABLE V

SEED COLLECTED AT LIBBY, MONTANA, OCTOBER 18, 1911; PRIEST RIVER, IDAHO, OCTOBER 1, 1912; AND AT COEUR D'ALENE, IDAHO, NOVEMBER 14,1914, FROM *R. americana* ON *Pinus contorta*.

TRIAL HOSTS			LOCALITY WHERE CULTURES WERE MADE AND DATE	RESULTS OF CULTURES	
Name and number used in cultures	Source of seed	Locality grown		Date of first observation of germination	Results (measurements averaged)
Pinus contorta (4)	Local	Local	Blue Lake, Idaho 10–2–12*	6–18–13	April 13 and October 14, 1916: 1 infection on each tree, slight swelling of branch on stem, 2 staminate, 2 pistillate (no. 666), not varying in any marked degree from parent plants.
Pinus ponderosa (4)......	Local	Local	Blue Lake, Idaho 10–2–12*	6–18–13	April 13, 1916: 2 infections at the same node on a single stem, only 1 tree infected, plants staminate and pistillate; former 4 cm. high, stems olive yellow; latter 5 cm. high, stems yellowish olive, fruit light dull glaucous blue (no. 667); parent; staminate, 8 cm. high, light yellowish olive with older parts of stem deep grape green; pistillate, 4 cm. high, uniformly dark olive gray, both stems and fruit (no. 668).
Pinus ponderosa (1)......	Mont.	Mont.	Missoula, Mont. 1–12–15†	2–16–15	October 10, 1915: 1 infection, slight swelling, branch died, plants did not appear.
Pinus montana (dwarf form) (4)	Europe	Spokane	Spokane, Wash. 11–10–11*	....	December 14, 1916: 1 infection; staminate, 5 mm. high, pronounced swelling of branch, excessive infiltration of resin, 2 small plants barely appeared in 1915, died out; another plant appeared just above original point of infection but remained small (no. 669).

* Cultures in field. † Greenhouse.

Montana. The parasite in this case caused unusually large and elongated swellings on the main stem of young trees, but the plants apparently were never able to come to maturity, remaining about 5–8 mm. high. One of the pines was transplanted into the greenhouse, and the context of the swelling shriveled up in a manner indicating that it was composed of very spongy tissues. The tree, however, remained living. The fact that 220 seeds of *R. americana* were sown on 6 different species of white pines with no result except the germination of the seeds further supports this observation. The trees tested were *Pinus Lambertiana*, *P. monticola*, *P. Strobus*, *P. edulis*, *P. cembroides*, and *P. Cembra*. *R. americana* is reported by COULTER and NELSON[8] on *Pinus flexilis*. The results of sowings on *Larix europea*, *L. occidentalis*, *Picea sitchensis*, *P. Engelmanni*, *P. excelsea*, *Abies nobilis*, *A. lasiocarpa*, *A. grandis*, *Tsuga heterophylla*, *Pseudotsuga taxifolia*, *Thuja plicata*, *Taxus brevifolia*, *Populus trichocarpa*, *Betula occidentalis*, and *Alnus tenuifolia* were negative.

SUMMARY.—The hosts of *Razoumofskya americana* are *Pinus contorta*, *P. Banksiana*, *P. attenuata*, *P. Jeffreyi*, *P. montana*, *P. ponderosa*, *P. flexilis*, and with difficulty *P. albicaulis*. The plant is of economic importance so far as known only on the two first named species. Morphological changes are induced by change of host or condition of growth, but not to an extent that this, the most characteristic of all members of the genus on pines, could be confused.

Cultures with hemlock mistletoe

In the St. Joe National Forest, Idaho, are several areas of almost pure stands of *Tsuga heterophylla* heavily infected with *R. tsugensis* (figs. 18, 19). In the border zones of these areas a form of mistletoe has been collected on *Abies grandis* and *A. lasiocarpa* which varies in a number of details from the form collected on the same hosts in regions where the large mistletoe on *Pinus ponderosa* occurs. In order to see whether this is a case of *R. tsugensis* infecting other hosts than the common western hemlock, and also to determine its host range in general, the cultures given in table VI were made.

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[8] New Manual of Botany of the Rocky Mountains. 146. 1909.

R. tsugensis is not confined to species of *Tsuga* as heretofore believed, but will infect *Abies lasiocarpa*. The mistletoe most closely resembling *R. tsugensis* in point of color and size is the form *R. occidentalis abietina*, but as the results from cultures stand at present there is apparently no relation between them. The foregoing results indicate that the plant occasionally found on firs in the same vicinity with *R. tsugensis* is the common hemlock mistletoe, and also that this species may be expected to occur occasionally on other hosts than hemlock. Cultures may be considered fully completed when the plants found on *Abies* in the vicinity of *R. tsugensis*, also the form on *Abies* which has been referred to the yellow pine mistletoe, are shown by culture to infect *Tsuga* and *Pinus* respectively.

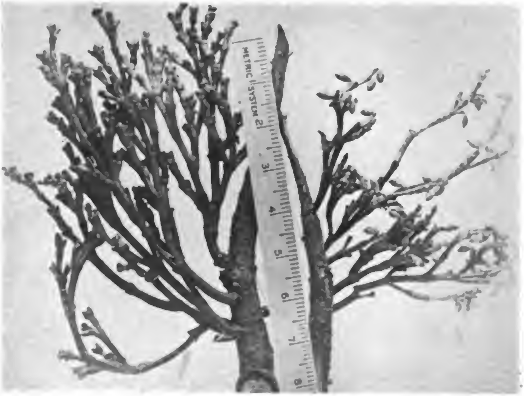

FIG. 18.—*R. tsugensis* on *Tsuga heterophylla:* staminate and pistillate plants; large form.

SUMMARY.—Seeds were also sown on *Abies grandis*, *Pinus ponderosa*, *Picea orientalis*, *Larix occidentalis*, and *Pseudotsuga taxifolia*, but the results were negative. The hosts of *Razoumofskya* *tsugensis* are *Tsuga heterophylla*, *Tsuga canadensis*, and *Abies lasiocarpa*. So far as the present cultures show, the hemlock mistletoe will not infect *Pinus*, *Picea*, *Larix*, and *Pseudotsuga*. The fact that this mistletoe will infect *Tsuga canadensis* indicates the possibility of it becoming a pest in the native regions of other species of hemlock and is a condition to be guarded against.

Conclusion

Cultures at present indicate that *R. campylopoda* and *R. cryptopoda* are not identical. Each form may exhibit considerable variation, due to geographic location and host. It is shown that *R. campylopoda* will infect *Pinus resinosa*, and care must be taken to prevent it from getting a foothold in the eastern United States. It will also infect *Pinus sylvestris* and *P. montana*, and should be prevented from entering Europe or plantations of these trees in America. It is also indicated that the plant known as *R. occidentalis abietina* is a biological form of *R. campylopoda*.

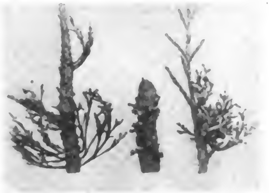

FIG. 19.—*R. tsugensis* on *Tsuga mertensiana:* staminate (center) and pistillate plants; small form; reduced one-half.

R. laricis will infect *Larix europea*, *L. leptolepis*, *Abies grandis*, *Pinus ponderosa*, and *P. contorta*. All are new hosts for this species except the last. The parasite apparently readily infects the Japanese and European larch and would be expected to cause serious damage to these trees. *Abies grandis*, *Pinus contorta*, and *P. ponderosa* are infected with difficulty. This parasite so far as known at present is of economic importance only on *Larix occidentalis*.

The mistletoe known under the name *R. Douglasii abietina* is shown to be identical with *R. Douglasii* and should be written under the latter name. *R. Douglasii* is only of importance on *Pseudotsuga taxifolia*.

TABLE VI

SEED COLLECTED AT MISSOULA, MONTANA, JANUARY 22, 1915, ADHERING TO BROOMS AND MISTLETOE PLANTS ON *Tsuga heterophylla* SENT FROM ASHFORD, WASHINGTON, AND FROM THE SAME HOST IN ST. JOE NATIONAL FOREST, IDAHO, SEPTEMBER 30, 1914

TRIAL HOSTS			LOCALITY WHERE CULTURES WERE MADE AND DATE	RESULTS OF CULTURES	
Name and number used in cultures	Source of seed	Locality grown		Date of first observation of germination	Results (measurements averaged)
Abies lasiocarpa (1)......	Mont.	Mont.	Missoula, Mont. 1-28-15†	2-29-16	January 3, 1917: 1 infection, staminate, 2 cm. high, leaf green (no. 686); parent, 6 cm. high, light yellowish olive.
Tsuga canadensis (1).....	Wis.	Wis.	Spokane, Wash. 10-7-13*	5-1-15	October 12, 1916: 1 infection, staminate, very slight swelling, 4 cm. high, dark greenish olive (no. 682); parent light brownish olive (no. 683).

* Cultures in field. † Greenhouse.

R. americana will infect both hard and soft pines, the latter with difficulty, and is of importance only on *Pinus contorta* and *P. Banksiana* of the former group. This mistletoe will infect *Pinus montana* and may be of consequence if introduced into Europe.

R. tsugensis will infect *Abies lasiocarpa*, thus possibly explaining the position of certain rare plants occasionally found on *Abies* in the vicinity of the hemlock mistletoe. This parasite will infect *Tsuga canadensis* and would probably cause serious damage to this tree in the East.

Cultures show very clearly that many of the characters employed in the classification of the false mistletoes vary with change of host, geographical location, and with various other environmental factors. This indicates that only the broader and plainly evident lines of demarcation should be employed in their classification.

Office of Investigation in Forest Pathology
Bureau of Plant Industry
Missoula, Mont.

CHEMICAL CHANGES ACCOMPANYING ABSCISSION IN COLEUS BLUMEI

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 240

HOMER C. SAMPSON

Introduction

VON MOHL (13) in 1860 was the first to announce that previous to the fall of the leaf there is formed near the base of the petiole a definite separation layer in which abscission always occurs by the separation of the cells from each other with their walls still intact. The xylem tubes not being included in this separation layer are finally ruptured mechanically, and the leaf falls. He also called attention to the fact that abscission and the formation of a protective tissue are two very distinct processes, and that the latter process might either precede or follow the former. WIESNER (17) in 1871 confirmed the observation of VON MOHL in the main, and formulated the theory that the dissolution of the intercellular substance of the cells of the separation layer is caused by the action of organic acids developed in the leaves. In 1886 MOLISCH (14) suggested that a gum ferment might be the cause of this dissolution process. Two years later MANGIN (11), upon his discovery of the pectic nature of the middle lamella of cell walls in plants, indirectly advanced the knowledge of abscission. Since this discovery the abscission process has generally been referred to as a dissolution of the pectose and calcium pectate of the middle lamella. LLOYD (8, 9), assuming the organic acid theory of WIESNER, speaks of the process as a hydrolysis of these pectic compounds, and later (11) of cellulose also.

The anatomical workers disagree somewhat on the amount of the cell wall altered during abscission. LEE (7) in 1911 reported the disappearance of the middle lamella only, and two years later HANNIG (6) reported the same condition in the abscission of flowers, with the exception of a species of *Mirabilis* and of *Oxybaphus*, in which the entire cell wall disappeared. On the other hand, TISON

(**15**) as early as 1900, working with numerous species studied later by LEE, stated that in general the secondary membranes of the cell wall also undergo alteration and disappear, leaving only the thin tertiary membrane lining the cell lumen. LLOYD (**9, 10**) has recently found the same condition in the abscission of cotton bolls and also in *Mirabilis*, instead of the disappearance of the entire cell wall as reported by HANNIG. It seems improbable that the presence of weak organic acids would be sufficient to account for this extreme alteration of the cellulose walls of these cells. Certain authors have suggested that the catalytic effect of enzymes may be an important factor in abscission, but experimental evidence has been wanting.

Aside from his organic acid theory, WIESNER (**21**) in 1905 suggested increased turgor as a cause of abscission under conditions of forced leaf-fall. FITTING (**5**) in 1911 accepts this view to account for the rapid abscission of petals when forced. The suggestion lacks experimental confirmation, and the work of HANNIG (**6**) indicates less need for its assumption.

The external factors capable of accelerating leaf-fall are extremely diversified. These have been summarized in the main by LLOYD (**8**). The more important are high and low light intensity, high and low water supply, high temperatures and frost, low concentrations of anesthetics, toxic concentrations of acids and salts, and wounding of the blade. On the other hand, low concentrations of oxygen and high concentrations of anesthetics retard leaf-fall, a state of rigor being produced by the latter.

The internal changes affected by these various external factors have received very little critical study. The work discussed in the present paper was undertaken to determine some of the internal changes accompanying abscission of leaves in *Coleus Blumei* var. Golden Bedder. This plant was chosen for study partly on account of its ease of propagation, but mainly for its simplicity of analysis owing to the absence of protective tissue at the time of abscission.

Anatomy

In order to appreciate fully the chemical changes taking place in the abscission layer, it is necessary not only to compare the abscission layer with the adjacent regions of the petiole, but also to follow the changes in the abscission layer itself from the time of its formation to the fall of the leaf. This latter process is most easily accomplished in *Coleus* by beginning with the terminal bud and taking the leaves as they appear in order down the stem, from the youngest to the oldest. On this basis the following description is applicable to *Coleus* plants growing in 4-inch pots under greenhouse conditions, with each plant bearing 8 pairs of leaves, and with the eighth pair in the process of abscissing.

In the first 2 pairs of leaves below the terminal bud there is no evidence of an abscission layer. The cells in the region where the abscission layer is later to occur are in the enlargement period of growth. The formation of the abscission layer in *Coleus* is usually initiated in the third pair of leaves below the terminal bud. Cell divisions in 2–4 layers of cells across the base of the petiole of these leaves begin in the epidermal and cortical region and gradually extend inward, reaching the phloem about the time the leaves appear as the fifth pair in order below the terminal bud. In the sixth pair of leaves the formation of the abscission layer is practically completed and involves all the tissue of the petiole except the xylem tubes. Growth of the leaf in general ceases long before this period is reached. In the majority of cases the fourth pair of leaves below the terminal bud are fully expanded. The formation of the abscission layer in *Coleus* therefore begins a short time before the maturity of the leaf and continues for a considerable period afterward. As a rule the layer is 8–12 cells in thickness. These cells always remain smaller than the neighboring cells of the adjacent regions of the petiole and their walls are somewhat thinner. At the time of abscission alteration of the walls of the cells of the abscission layer is quite general, but a continuous plane of separation is finally formed somewhat nearer the distal side of this layer. This extreme alteration of cell walls is localized in the abscission layer and is not found throughout the entire leaf, as was reported by WIESNER (**18**).

While this description is true in general for *Coleus* plants bearing 8 pairs of leaves, slight variations are not infrequent. The stages of development may be either retarded or accelerated. Under conditions of forced leaf-fall all processes are greatly accelerated. The data in table I show that all processes, including the process of abscission, may be completed in the third pair of leaves in a period of 2 or 3 days as a result of the amputation of the blades. On the other hand, amputation of the blades of the first and second pairs of leaves before the beginning of the formation of the abscission layer inhibits its formation entirely.

Method of abscission

UNDER ORDINARY GROWING CONDITIONS.—The method of abscission has received much attention, but a critical survey of the exact changes in the cellulose and pectic compounds is wanting. An attempt to follow these changes in *Coleus* led to the discovery of certain facts which have a direct bearing upon the existing theories of the cause of abscission.

Microchemical analyses show that there is a breaking down not only of the calcium pectate of the middle lamella of the cells of the separation layer, but also of the cellulose of the secondary membrane, leaving only a thin layer of cellulose surrounding the lumen of the cells. This cellulose is first changed to pectose, which, according to CROSS (1), TOLLENS (16), and EULER (3), contains more oxygen than cellulose and probably is an oxidized form. The pectose is then further changed to pectin and pectic acid; the excess pectic acid becomes gelatinous and is no longer able to hold the cells together, and the leaf falls. The changes taking place in the walls of the xylem tubes are still to be investigated. During this process there is not a disappearance of calcium from the cell walls, but the excess of pectic acid produced renders the amount of calcium present insufficient to maintain the solidity of this portion of the cell wall. The excess pectic acid appears to come from the transformation of the pectose rather than from the breaking down of the calcium pectate of the middle lamella. Since this description differs from all previous accounts of the method of abscission, further discussion is postponed until all the facts are brought together under the topic of microchemical analysis.

FORCED LEAF-FALL.—Leaf-fall was accelerated by treatment with ethylene, amputation of the blade, and by allowing the soil to become dry and then suddenly applying an excess of water. Under the first two treatments the leaves began to fall within 24 hours.

The rate of petiole fall after the amputation of the blade is shown in table I. At the beginning of the experiment each plant had 8 pairs of leaves and 1 blade of each pair was removed. The numbers refer to the total number of abscissed petioles at the corresponding dates.

TABLE I

RATE OF PETIOLE FALL FOLLOWING AMPUTATION OF BLADES

Plant	January					February		March							
	27	28	29	30	31	1	2	1	2	3	4	5	6	7	10
A*	1	5	....	....	....	....	6	6	....	....	....	....	....	....	6
B*	1	4	....	5	....	....	6	6	....	....	....	....	....	....	6
C†	....	....	....	....	....	....	....	....	3	4	6	....	....	6	....
D†	....	....	....	....	....	....	....	....	4	5	....	....	....	6	....
E†	....	....	....	....	....	....	....	....	4	6	6	....	....	6	....

* Blades amputated January 26; † blades amputated March 1.

A microchemical analysis of the abscission layer in all these cases showed exactly the same changes in cellulose and pectic substances as noted under ordinary conditions of growth. Furthermore, changes in oxidases, calcium in solution, and iron, to be discussed later, were the same in all cases. These facts emphasize again the need of experimental investigation before accepting the turgor pressure theory of the cause of abscission.

It is interesting to note that while the petioles usually absciss soon after amputation of the blade, there is one striking exception. If the blade is removed before the abscission layer is initiated, growth ceases throughout the entire petiole, the layer fails to develop, and the petiole is not dropped. The data in table I show that the 6 lowest petioles soon fall, but the upper 2 remain attached. This is an easy method of locating the period of formation of the abscission layer. This extreme cessation of growth in the petiole induced by artificial means has some features in common with a retardation of growth and abscission formation in the petioles of the upper leaves under natural conditions of flowering and fruiting. As a result of slowing up of growth and formation of abscission layers in the petioles of the upper 3–5 pairs of leaves accompanying the development of the floral axis, these leaves remain on during the entire flowering and fruiting period. An investigation of the internal changes accompanying these 2 phenomena may throw some light upon abscission in general.

Organic acids as a cause of leaf-fall

WIESNER (17–21) cites three lines of experimental evidence as proof that the dissolution of the middle lamella is a result of the accumulation of organic acids in the aging leaves: (1) yellow leaves macerated and extracted with water when titrated were more acid than green leaves; (2) cuttings placed in 2.5 per cent oxalic acid dropped their leaves in a few days; (3) the exposed abscission surface of the petiole always gives an acid reaction to neutral red.

Abscission in *Coleus* when examined from the point of view of this theory shows several facts in disagreement and not one in its favor. Cuttings placed in non-toxic concentrations of oxalic acid showed no acceleration of leaf-fall over that of cuttings in distilled water. Cuttings in 0.0002 N oxalic acid showed slight toxic effects. The immersed part of the stem and the tips of young leaves on axillary branches became brown in color. The concentration of acid used by WIESNER was 1500 times as great, but he fails to state what plants were used and whether toxic effects were produced. Cuttings of *Coleus* in 0.0016 N oxalic acid did not show an acceleration of leaf-fall, although the toxic effects were strongly pronounced. It was further found that the plants soon became adjusted to the oxalic acid. Plants started in 0.0002 N oxalic acid were transferred every third day to a concentration of acid double that of the previous concentration. This was continued until the plants were finally placed in 0.0512 N oxalic acid. There was no acceleration of leaf-fall during the entire period. At the end of the treatment the cells of the plant were found to be filled with starch.

Similarly, potted plants infiltrated with non-toxic concentrations of oxalic acid showed no acceleration in leaf-fall. The plants were inverted under bell jars in vessels containing the various solutions, and the air was exhausted to 3 cm. of mercury. The volume of solution entering the infiltrated plant was approximately equal to one-fourth the volume of the plant. No toxic effects were noted for concentrations of 0.0064 N oxalic acid and below. The results are given in table II.

TABLE II

SHOWING EFFECT OF DIFFERENT CONCENTRATIONS OF OXALIC ACID ON RATE OF ABSCISSION

Concentration	February														March				
	15	16	17	18	19	20	21	22	23	24	25	26	27	28	1	2	3	4	5
0.0256 N oxalic acid										2		3		4	5		6		
0.0128 " " "								2				3		5			6		
0.0064 " " "	1							2		3				4	5		6		
0.0032 " " "			1									2		5					6
0.0016 " " "										1				2	3	4	5	6	
0.0008 " " "								1		2				3		4	5	6	
0.0004 " " "										2				4	6	7		8	
Untreated										3		4		6	7				8
"			1							3		4		6		8			

The plants were infiltrated February 9, and again February 22. Leaf-fall was allowed to occur normally under greenhouse conditions. The numbers refer to the total number of leaves off at the corresponding date.

Although concentrations of 0.0128 and 0.0256 N oxalic acid showed marked toxic effects, abscission was not accelerated; concentrations between 0.04 and 0.12 N oxalic acid killed many blades without killing the petioles and stem. In such cases abscission of the petioles occurred within 2 or 3 days, just as in the case of petiole fall after amputation of the blade, or severe wounding of the blade.

Likewise direct measurements of acidity do not agree with those of WIESNER. Table IV gives the acidity for 9 different regions of the plant. Falling leaves are not so acid as green leaves. Fresh yellow leaves in the act of abscissing when titrated with NaOH, using phenolphthalein as an indicator, had an acidity equivalent to 0.0069 cc. of normal acid per gram of wet weight. Fresh green leaves collected at the same time from the same plants had an acidity equivalent to 0.0089 cc. of normal acid per gram of wet weight. In both cases the leaves were weighed as rapidly as possible after collecting, macerated in a mortar, made up to volume with distilled water, and after shaking for 30 minutes the solutions were filtered through a Buchner funnel and definite portions taken for titration. Fresh abscission layers treated in this way had an acidity of 0.0100 cc. per gram of wet weight, while that of the adjacent part of the petiole was 0.0095 cc. These two figures are not to be compared with those preceding, as the two sets of titrations were made at different times and on different plants.

If the calcium pectate were being hydrolyzed by an organic acid, one would expect to find either an increase of calcium in solution in the cells of the abscission layer or an increase of crystals of calcium compounds in these cells. Such is not the case. Neither are there any calcium oxalate crystals in the middle lamella of these cells, such as one finds when the middle lamella is broken down by adding oxalic acid to sections under the microscope.

Finally, the marked acidity of the abscission surface of a falling leaf was certainly not correctly interpreted by WIESNER. He ascribes the acidity of the abscission surface to the excretion of organic acids from the interior of the cells. This abscission surface is a continuous layer of pectic acid, formed during the abscission process, and the acidity of the abscission surface, therefore, is a result of the formation of pectic acid during abscission, and not of the escape of acids previously formed in the cells. This acidity of the middle lamella to neutral red may be seen in *Coleus* in any part of the plant, and it is increased in the walls of the abscission layer only after the formation of pectic acid during abscission.

In conclusion, therefore, neither the turgor pressure theory nor the organic acid theory proposed by WIESNER to account for the cause of leaf-fall is in accordance with the facts observed in *Coleus*.

Effect of salts on leaf-fall

According to CZAPEK (2), the membranes of plant cells are colloidal in nature, and MANGIN has shown that the middle lamella is composed of pectic acid in combination with calcium. During the process of abscission the middle lamella undergoes a chemical alteration and the pectic acid present takes up water and swells. It was expected, therefore, that salts might show either a lyotropic effect on the intake of water by the pectic acid or a specific effect of salt formation with this acid and thus affect the course of abscission. The following anions were used in the form of their potassium and calcium salts: PO_4, SO_4, Cl, NO_3, and CNS; and the following cations in the form of their chlorides: K, Na, Ca, Ba. In all cases 0.01 normal concentrations were used. The plants were treated by infiltration, by placing cuttings directly in the solutions, and by adding the salts to the soil. Abscission was slightly accelerated by treating the plants with 4 parts of ethylene per million of air. In all cases the results were the same. Neither lyotropic nor specific effects were noted. Similarly, concentrations of potassium and calcium chlorides between 0.04 and 0.00016 normal showed no marked effect.

The experiment was repeated under conditions of rapid acceleration of abscission by treating the plants with 700 parts of ethylene per million of air. The results which agree with those above are summarized in table III.

TABLE III

SHOWING EFFECT OF SALTS ON ABSCISSION

CONCENTRATION	FEBRUARY 12	FEBRUARY 15		FEBRUARY 14		FEBRUARY 13	
	5 P.M.	9 A.M.	5 P.M.	9 A.M.	5 P.M.	9 A.M.	5 P.M.
0.01 N KH_2PO_4		1		3	5		5
" " K_2SO_4			2	3	4		4
" " $CaSO_4$			5	6			6
" " KCl			3	4	5		5
" " KNO_3		2	3	5			5
" " $Ca(NO_3)_2$				2		4	4
" " KCNS		1		3		4	4
Untreated		2			3	4	4
"	2	5	6				6
"				2		3	3
"		1		4		6	6
"		3		4		6	6
0.01 N KCl			3	4	5		5
" " NaCl			3	4	4		4
" " $CaCl_2$				4	4		4
" " $BaCl_2$			2	4	4		4

Cuttings in solutions of the different salts gave similar results. The great diversity of the checks noted in this table is very unusual.

The failure of calcium to show a specific effect was unexpected. Later work, however, has thrown some light upon the matter, and it will be discussed under microchemical analysis.

Oxygen pressure and leaf-fall

Molisch (14) grew plants half submersed in water and found that the aerial portions dropped their leaves sooner than the submersed portions. From this fact he concluded that low oxygen pressure retarded leaf-fall. This surmise proved to be correct. *Coleus* plants grown in a hydrogen atmosphere under bell jars with only sufficient oxygen to maintain a slow growth retain their leaves much longer than plants in normal air. Under conditions of the experiment the plants in normal air usually retain 8 pairs of leaves. In the hydrogen atmosphere the plant retained 11 pairs of leaves. Inception of decay at the base of the stem destroyed the experiment at this point. Similarly, petiole fall, after amputation of the blade, is greatly retarded in very low concentrations of oxygen. Plants grown in 0.1 normal oxygen pressure showed no retardation of leaf-fall. Whether the effect of oxygen in such cases is that of an essential factor influencing the general metabolism of the plant, or of a formative factor influencing directly the oxidase activity in the abscission layer, or of both acting simultaneously, is a problem still to be investigated. Likewise a critical investigation of the possibility of a double effect of carbon dioxide on leaf-fall might throw more light upon the causes underlying abscission.

Macrochemical analysis

In order to follow the chemical changes leading up to abscission, both macrochemical and microchemical methods of analysis were employed. About 2500 plants grown under greenhouse conditions were used for the macrochemical analysis. These plants were all grown at the same time under the same conditions, and collection of material was made at the same time each day. Series C was collected between February 17 and March 3, collections being taken from day to day as the lower leaves began to absciss. Series D and E were collected from these same plants on March 3 and 4.

Material when collected was placed in 70–80 per cent alcohol and heated to 70°C. for one hour to destroy enzymatic activity.

The material was then extracted with alcohol and ether. The residue was dried and analyzed for polysaccharides, calcium, and oxalates. The alcohol-ether extract was evaporated to dryness on a steam bath and then extracted with water at 70°C. The filtrate of this aqueous extract was analyzed for reducing and non-reducing sugars; ammonia, amino acid, and nitrate nitrogen; calcium in solution, and acidity.

Table IV gives a summary of an analysis of 9 different regions of the plant. Series C represents leaves in the act of abscissing, series E represents leaves at the time of the formation of the abscission layer, and series D represents leaves intermediate between these two points. Collection E1 represents approximately 5 mm. of the abscission end of the petiole, collection E2 an equal portion of the adjacent part of the petiole, and collection E3 a portion of the blades. In like manner, collections C1, C2, and C3 and collections D1, D2, and D3 represent these same three regions in their respective series.

Attention should be called to the fact that while collections C1, D1, and E1 represent the abscission end of the petiole, they do not represent the abscission layer only. In no case does the abscission layer represent more than about 5 or 6 per cent of the portion of the petiole taken. In collection C1 it represents still less, probably not more than 2 per cent, as in the abscissing leaf the petiole retains only about one-third of the abscission layer, the remaining two-thirds being attached to the stem.

It is evident that chemical changes in the abscission layer might be overshadowed by the remaining 95 per cent of the collection, and even more so in collection C1 than in collections D1 and E1. This is especially true of the nitrates, which are frequently confined almost entirely to the abscission layer and are more abundant in this layer at the time of abscission than at any other time, although the figures in the table might lead one to think they were most abundant a short time before abscission. As a matter of fact, a large percentage of the nitrates in the abscission layer of collection C1 were left in the part of the abscission layer remaining attached

TABLE IV

COLLECTION	PERCENTAGE DRY WEIGHT	PERCENTAGE OF DRY MATERIAL			EXPRESSED AS PERCENTAGE OF TOTAL DRY WEIGHT											TOTAL ACIDITY AS NORMAL ACID (IN CC.) PER GRAIN OF WET WEIGHT
		Water soluble	Alcohol-ether soluble	Alcohol-ether but not water soluble	Total carbo-hydrates	Polysaccharides	Non-reducing disaccharides	Reducing substances	NH_3 nitrogen	Amino acid nitrogen	NO_3 nitrogen	Total calcium	Calcium in solution	Calcium not in solution	Oxalates as anhydrous oxalic acid	
E1	3.94	28.92	31.55	2.63	11.89	11.44	0.0	0.45	0.063	0.106	0.900	3.06	0.17	2.89	1.97	0.0068
E2	3.95	28.76	32.04	3.28	13.23	12.33	0.0	0.90	0.048	0.033	0.042	3.20	0.20	3.00	2.07	0.0079
E3	7.43	13.23	22.76	9.53	17.04	15.09	0.13	1.82	0.020	0.056	0.140	2.18	0.06	2.12	1.34	0.0057
D1	3.61	30.85	35.30	4.54	14.02	11.88	0.40	1.74	0.076	0.097	2.820	3.07	0.37	2.70	1.41	0.0073
D2	3.20	...	33.32	......	14.03	12.03	0.0	2.00	0.072	0.057	0.180	3.42	0.33	3.09	1.31	0.0058
D3	6.74	17.54	26.00	8.46	24.00	19.70	0.0	4.27	0.009	0.058	0.037	2.52	0.09	2.43	1.47	0.0100
C1	4.33	25.56	45.96	20.40	13.21	10.95	0.0	2.26	0.030	0.080	1.670	2.32	0.12	2.20	2.07	0.0069
C2	3.33	29.44	32.97	3.53	15.02	10.42	0.0	4.60	0.036	0.078	0.950	3.06	0.21	2.85	1.70	0.0055
C3	5.06	19.85	27.34	7.49	15.82	10.88	0.58	4.35	0.024	0.072	0.036	3.61	0.12	3.49	2.02	0.0065

to the stem, and therefore are not included in the analyses. The data in the table, therefore, represent only the general chemical changes during the life of the leaves, while the detailed chemical changes occurring in the abscission layer itself will be given under microchemical analysis. Should one desire to make a macrochemical analysis of the abscission layers alone in *Coleus* no less than 40,000 plants would be needed.

The data in table IV show an increase in dry weight in the abscission end of the petiole at the time of abscission; also an increase in alcohol-ether soluble material, but no increase in water soluble material. The significance of these changes is uncertain. In the older petioles there is a slight decrease in polysaccharides and an increase in reducing substances. There is no increase in ammonia and amino acids, as might be expected if the protoplasm were breaking down. Oxalates and total calcium remain fairly constant, but there is a slight decrease in the amount of calcium in solution and in the acidity. A more detailed discussion of the chemical changes in the abscission layer is given under microchemical analysis.

In the older blades there is a decided decrease in the amount of accumulated starch at the time of abscission, but the amount of reducing substances remains fairly constant. Attention has already been called to the fact that the formation of the abscission layer is completed while the leaf is still in an active photosynthetic condition. Both photosynthesis and the translocation of foods continue for several days or weeks later. The data clearly show that the presence of the abscission layer does not prevent the movement of water and foods between leaf and stem.

Microchemical analysis

A microchemical investigation of *Coleus* showed a striking localization of physical and chemical changes in the abscission layer shortly before and at the time of abscission. The formation of the abscission layer usually in the third pair of leaves and the occurrence of abscission usually in the eighth pair of leaves (when the plants are grown in 4-inch pots in a greenhouse) make it possible to study the whole history of the abscission layer by investigation of only 6 pairs of leaves in each plant. The fact that the leaves are opposite is also of advantage. Abscission of the pair may occur simultaneously, or one of the pair may absciss long before the other begins, or it may occur at any stage in between. Since both abscission layers at each node may readily be obtained in a single free-hand section, it is possible to contrast all stages of abscission under exactly the same treatment. A study of the changes induced by forcing abscission in one of the leaves at each node is likewise facilitated.

The investigations completed include a study of the distribution and amount of nitrates, carbohydrates, oxidases, iron, manganese, calcium in solution, and oxalates.

NITRATES.—The data in table IV show a great increase of nitrates in the abscission end of the petiole as compared with the remainder of the leaf. Furthermore, the nitrates in this part of the petiole are least abundant at the time of formation of the abscission layer and most abundant a short time before leaf-fall. As already noted, these figures cannot be taken to represent the percentage of nitrates in the abscission layer. Microchemical tests show some interesting variations. In many plants the increase in nitrates is confined almost entirely to the abscission layer, while in others the petiole or the neighboring part of the stem may also show a like increase. In all cases studied there is an increase in nitrates in the abscission layer just before and at the time of abscission. In some plants this increase is gradual from the time of the formation of the abscission layer to the time of abscission. In other cases only traces of nitrates appear in the abscission layer until a short time before abscission, when they increase rather suddenly.

CARBOHYDRATES.—The data in table IV show that the free reducing sugars, like the nitrates, increase in the abscission end of the petiole with the increase in the age of the leaves, but, unlike the nitrates, they are less abundant in this part of the petiole than in the remainder of the leaf. This correlation of the amount of reducing sugars and the age of the tissue is still more striking when studied microchemically. From the terminal bud to the oldest leaves there is a gradual increase in reducing sugars in both stems and leaves. This increase is initiated last in the abscission layer.

As a result the abscission layer has a lower percentage of reducing sugars throughout its entire history than the adjacent regions of the petiole. This difference is most marked in the fifth and sixth pairs of leaves near the close of the formation of the abscission layer, but it is still quite evident at the time of abscission. In the cell walls of the abscission layer the change in form of the carbohydrates is still more pronounced and significant. During the process of abscission the first evident change in the cell walls is a conversion of cellulose of the secondary cell membranes to pectose. The second step is a conversion of some of this pectose to pectic acid and pectin. This is followed by the breaking down of the middle lamella of calcium pectate and the separation of the cells. The changes from cellulose to pectose can readily be followed by differential staining and crystallization methods, and by solubility tests. The evidence of the conversion of pectose to pectin and pectic acid is based upon solubility tests. Pectin is soluble in water, pectic acid is insoluble in water but soluble in dilute alkalies, while pectose is insoluble in both water and dilute alkalies. When an abscission layer at the time of abscission is treated with 3 per cent ammonium or potassium hydroxide or with 5 per cent sodium carbonate, the free pectic acid is dissolved. If the walls are then again examined a considerable portion of the secondary membrane, bordering the middle lamella which is still intact, is seen to have disappeared. A discussion of the changes in the calcium pectate is postponed until all the remaining facts have been stated.

OXIDASES.—In the stem and petioles oxidases are found in the epidermal and phloem tissues. In the abscission layer oxidases are found in all tissues except the xylem. Not only is this distribution peculiar to this region, but the increase in oxidases with the age of the abscission layer is also quite pronounced. Quantitative tests of the increase in oxidative activity are still to be made.

IRON.—Slight traces of iron (Fe^{+++}) are usually found throughout the plant, especially where chlorophyll is present. It is most abundant in the xylem tubes and in the epidermal region until a few hours before abscission, when it becomes extraordinarily abundant in the cells of the abscission layer. The path of diffusion of the iron leading to its accumulation in the abscission layer has not been traced. No manganese was found.

CALCIUM AND OXALATES.—The data in table IV show no marked difference in the distribution of oxalates in the leaves. Only occasional crystals of calcium oxalate are found in the cells, and none are found in the cell walls of the abscission layer at any time. Likewise the total calcium has a fairly constant distribution throughout the plant, but slight variations of the calcium in solution are to be noted. The most striking and significant changes of the amount of calcium in solution, however, are shown by microchemical tests. Treatment of sections with 50 per cent sulphuric acid or with 3 per cent oxalic acid or ammonium oxalate show an abundance of calcium in solution in all living cells of the petiole except those of the abscission layer at the time of abscission. The crystals of calcium sulphate or of calcium oxalate obtained by these treatments were very numerous in the cells of the abscission layer before the time of abscission, the latter averaging 30 crystals per cell, while during abscission only an occasional crystal was obtained. This decrease of calcium in solution is not always confined to the abscission layer, but breaks off rather abruptly in the first few layers of cells of the adjacent region of the petiole. In some cases cells not more than 5 cell layers distant from the line of cleavage showed no decrease in the number of crystals. These facts show that the calcium in solution in the abscission layer disappears during abscission, and it should be further stated that the disappearance takes place in the first stages of the process.

Summary of microchemical analysis

1. A pronounced increase in nitrates always occurs in the abscission layer at the time of abscission. This increase may be gradual, extending over the entire life-history of the abscission layer, or it may appear somewhat suddenly a short time before abscission.

2. A gradual increase in the amount of reducing sugars accompanies the aging of leaves and stem. This increase is initiated last and is least pronounced in the abscission layer.

3. During the process of abscission the cellulose of the secondary membrane of the cell walls of the abscission layer is converted into

pectose. This pectose is further transformed into pectic acid and pectin. The final stage is the breaking down of the calcium pectate of the middle lamella.

4. Oxidases are present in the epidermal and phloem tissues in both stems and petioles. In the abscission layer they are present in all tissues outside of the xylem, and increase in amount with the age of the abscission layer.

5. Slight traces of iron may be found in practically all parts of stem and petioles, but shortly before abscission there is a sudden accumulation of iron in the abscission layer.

6. The amount of oxalates remains fairly constant throughout the entire life of the leaves. There is no evidence of an increase of calcium oxalate crystals in the cells of the abscission layer at the time of abscission, nor are there any crystals of calcium oxalate in the walls of these cells.

7. Calcium in solution is abundant in all living cells of the plant except those of the abscission layer at the time of abscission, where it practically disappears.

Discussion

According to TOLLENS (**16**), pectose is an oxidized cellulose of the composition $9(C_6H_{10}O_5)-C_6H_{10}O_6$. The first step in the breaking down of the cell walls in abscission in *Coleus* is evidently one of oxidation of cellulose. This process is possibly a result of the accumulation and subsequent activity of oxidases in the abscission layer, and also of the catalytic action of iron on these oxidases. This may be merely an acceleration of the conversion of cellulose into pectose which ordinarily goes on in cell walls of plants with increasing age. Cellulases may play a part in this process, but the question is still to be investigated. EULER (**4**) succeeded in isolating a cellulase in a fungus, *Merulius lacrimans*, which was capable of altering cellulose, but cellulases in higher plants are still unknown. CZAPEK (**2**) and EULER (**3**) have called attention to the fact that our knowledge of cellulases is very limited.

The pectose formed from the cellulose is in turn readily transformed to pectic acid and pectin, and in this process the catalytic action of iron may again play an important rôle. Whether acids and pectic enzymes also play a rôle in these changes is uncertain. Hydrolytic action may underlie some or all of these changes, but this must remain an open question until the molecular composition of these compounds is definitely known. At any rate, the transformation of the cellulose and pectose leads to the formation of an excess of pectic acid in the cell walls of the abscission layer.

The most important question still open is the cause of the final breaking down of the calcium pectate of the middle lamella. There appear to be but two possibilities. Either the calcium ion of the pectate is captured by some anion, liberated in the cells of the abscission layer, and held in solution or precipitated, thus freeing the pectic acid, or the breaking down of the cellulose and pectose may lead to such an excess of pectic acid that the available calcium is no longer able to hold a sufficient proportion of the pectic acid as a salt, and thus maintain the solidity of the middle portion of the cell wall.

The fact that calcium is not found in solution in the cells of the abscission layer, nor in crystalline forms either in the cells or in the cell walls, is decidedly against the first view, which is simply WIESNER's organic acid theory stated in slightly different terms and which has already been discussed in detail.

The second view is more easily understood when we recall the well known law of physical-chemical equilibrium. As soon as an excess of pectic acid is present in contact with the calcium pectate of the middle lamella there is undoubtedly a diffusion of calcium ions from the middle lamella and a diffusion of pectic acid into the middle lamella until an equilibrium of distribution of the two ions is established. A critical proportion of pectic acid to calcium would be reached in the middle lamella when the excess pectic acid breaks the continuity of the calcium pectate layer. This second view has the further advantage of being in accordance with all the experimental facts so far known, particularly the formation of excess pectic acid in the cell walls and the paucity of calcium in solution in the cells of the abscission layer.

The fact already stated, in the discussion of calcium, that there is an abundance of calcium in solution in cells within 5 cell layers of the line of cleavage in abscission, indicates either that the process of abscission is a very rapid one or that the diffusion of calcium from cell to cell is a very slow one. This fact also explains why the addition of calcium salts, already discussed, showed no specific effects on the rate of leaf-fall as the rate of diffusion of the calcium ions through the cells would again appear as a limiting factor.

Extensive comparative investigations of abscission in the light of facts discovered in *Coleus* are still to be made. TISON'S statement that in general the secondary membranes also are altered in abscission indicates that these processes may be rather general, particularly since the reports of HANNIG and LLOYD of a similar alteration in the abscission of floral organs. Investigation of the more fundamental factors underlying the ultimate chemical changes discussed in this paper must be made before general conclusions of the causes leading up to abscission can be drawn. The significance of the presence of an abundance of nitrates in the abscission layer at the time of abscission is uncertain. Their ability to affect the water holding capacity of colloids and similar effects of other ions which are changing in concentration in this region may influence the permeability of the cell membranes of these cells, a question that has not yet been touched upon experimentally.

Conclusion

Abscission of leaves in *Coleus Blumei* is a result of the conversion of cellulose into pectose, which is further transformed to pectin and pectic acid, leading to the formation of an excess amount of pectic acid over that of the available calcium sufficient to maintain the solidity of the middle lamella of the cell walls of the abscission layer. These processes are possibly initiated and probably accelerated by the presence of oxidases and ferric ions, both of which accumulate in the abscission layer.

Microchemical methods employed

In the microchemical study color reactions were used for orientation. These were followed by specific chemical reactions and solubility tests. A brief outline of the tests made for each substance follows. Details of these reactions may be found in recent microchemical texts.

CELLULOSE.—(1) Chlorzinc iodide: blue color; (2) hydrocellulose reaction: blue color with iodine after treatment with 75 per cent sulphuric acid; (3) solubility: insoluble in dilute acids and alkalies, soluble in copper-oxide-ammonia; (4) crystallization: dissolve in copper-oxide-ammonia, wash with ammonia and water; colorless sphaero crystals or spiculate crystal clusters appear within the cells; (5) crystal reactions: insoluble in dilute acids and alkalies, soluble in copper-oxide-ammonia and sulphuric acid; blue color with chlorzinc iodide; (6) membranes of cellulose exhibit double refraction in polarized light.

PECTIC COMPOUNDS IN GENERAL.—(1) Ruthenium red: red color; (2) methylene blue: violet color; (3) membranes of pectic compounds do not exhibit double refraction in polarized light.

PECTOSE.—(1) Insoluble in copper-oxide-ammonia, dilute alkalies, ammonia, and alkali carbonates; (2) converted into pectic acid and pectin when gently heated with 2 per cent hydrochloric acid for 30 minutes. These latter substances are readily dissolved by 2 per cent potassium hydroxide or 5 per cent sodium carbonate, leaving the cellulose membrane intact.

PECTIC ACID.—(1) Soluble in dilute alkalies, ammonia, and alkali carbonates; (2) insoluble in water.

PECTIN.—Soluble in water.

CALCIUM PECTATE.—(1) Hydrolyzed by 2 per cent hydrochloric acid: calcium chloride is formed and pectic acid set free; (2) 3 per cent oxalic acid or ammonium oxalate: calcium oxalate crystals are formed, pectic acid set free; (3) 5 per cent sulphuric acid: calcium sulphate crystals formed, pectic acid set free.

CALCIUM.—(1) Two per cent oxalic acid: calcium oxalate crystals; (2) 5 per cent sulphuric acid: calcium sulphate crystals.

LIGNIN.—Phloroglucin-HCl reaction: red violet color.

SUBERIN.—(1) Sudan III or Scharlach R: red color; (2) insoluble in copper-oxide-ammonia; (3) phellonic acid reaction.

FRUCTOSE.—(1) Fluckiger's reaction: yellowish-red precipitate of cuprous oxide at once without heating; (2) phenylhydrazine reaction: yellow osazone crystals formed in 6–8 hours; (3) methylphenylhydrazine reaction: insoluble osazone; crystals formed in 15 minutes if preparation is heated, after 24 hours at room temperature.

GLUCOSE.—(1) Fluckiger's reaction: yellowish-red precipitate of cuprous oxide after heating 1–2 minutes; (2) phenylhydrazine reaction: yellow osazone crystals formed after about 24 hours.

SUCROSE.—Remove fructose and glucose. Invert with hydrochloric acid. Test for glucose and fructose as preceding.

NITRATE.—(1) Diphenylamine sulphuric acid reaction: blue color slowly changing to brown-yellow; (2) brucin-sulphuric acid reaction: red color.

OXIDASES.—Benzedine reaction: blue or purple precipitate if tissue is acid, soon changing to brown; brown precipitate at once if tissue is neutral or alkaline.

IRON.—(1) Berlin blue reaction: sections in 2 per cent solution of potassium ferrocyanide 15 minutes, add a drop of 2 per cent hydrochloric acid. A dark blue precipitate indicates the presence of ferric ions. Similarly a red color with potassium ferricyanide indicates the presence of ferrous ions; (2) sodium thiosulphate: red color.

MANGANESE.—Sections in 0.1 per cent hydrochloric acid, add 0.5 per cent sodium ammonium phosphate and ammonia vapor: ammonium manganese phosphate crystals, brown color in a 2 per cent solution of potassium permanganate.

MALIC ACID.—(1) Silver nitrate: sphaero crystals of silver nitrate, soluble in ammonia; (2) lead oxide: lead malate crystals; (3) sublimation: concentrated sulphuric acid, heat to 130°C.; slight charring.

OXALIC ACID.—(1) Uranium acetate: large yellow crystals of uranium oxalate; (2) strontium nitrate: strontium oxalate crystals; (3) ferrous phosphate: yellow precipitate of ferrous oxalate.

AMINO ACIDS.—Crystallization: treat sections with absolute alcohol, crystals of amino acids; (1) compare with known crystal form; (2) specific reactions.

TYROSINE.—Millon reaction: red color.

ARGININE, HISTIDINE.—Picrolonic acid: yellow crystalline precipitate.

LEUCINE.—Sublimation at 170°C.

ASPARAGINE, GLUTAMINE.—Quinone: red color.

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INTERRELATIONSHIPS OF THE TAXINEAE

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(WITH PLATES I, II)

In considering the Taxineae it is interesting to note the taxonomic position to which this subtribe has been assigned at various periods in the history of the classification of the conifers. **ENGLER** and **PRANTL** (4) in 1889 placed it at the top of the group; **PENHALLOW** (6) in 1907 placed it at the bottom of the group; **COULTER** and **CHAMBERLAIN** (1) in 1901 regarded the subtribe as the most primitive of the conifers and placed it at the bottom, but in 1910 (2) shifted its position to the top of the group as the most modern. These facts show clearly that the family is a difficult one to interpret, and the difficulty is due in part to the fact that the Taxineae combine at the same time extreme simplification and specialization.

The argument presented by **PENHALLOW** as evidence for his theory that the Taxineae are the most primitive of the conifers is based on the progressive development of the resin canals in *Pinus* and *Picea* from the isolated resin cells of *Podocarpus* "by various phases of aggregation." In *Taxus* and *Torreya* of the Taxineae, which he investigated, **PENHALLOW** states that resin cells are entirely wanting. Isolated resin cells occur in abundance in *Podocarpus* of the Taxineae. In the true Coniferae isolated or aggregated resin cells are characteristic of all the genera except *Picea* and *Pinus*, where they are replaced by resin passages, of which the aggregations of resin cells form an essential part. From the genera *Taxus* and *Torreya*, characterized by the absence of resin cells, **PENHALLOW** traces a series through *Podocarpus*, where resin cells are scattered, to genera of the Coniferae, where first, as in *Taxodium* and *Libocedrus*, the resin cells are arranged in well defined zones as well as scattered, to resin sacs in *Abies* and *Sequoia*, to resin passages with constrictions in the canal in *Larix*, *Pseudotsuga*, and *Picea*, to the resin passages without constrictions, as in *Pinus*.

Those who hold that the Taxineae represent a modern group in the evolution of the conifers interpret the facts already stated in PENHALLOW's argument as evidence of an entirely different progression. Starting with the genera in which the resin canal is highly specialized and resin cells wholly lacking, as in *Pinus*, they trace a series in which there is a gradual reduction of the resin canal, to aggregations of resin cells as in *Taxodium*, to scattered resin cells as in *Sequoia* and *Podocarpus*, to entire absence of resin cells as in *Taxus*.

As evidence of the fact that resin canals represent a primitive condition in the conifers, JEFFREY's work on the genus *Sequoia* may be cited. If the presence of resin canals were evidence of modern development, we should expect to find them in the mature and more progressive parts of the plant, but in *Sequoia gigantea* JEFFREY (**5**) found the resin canals only in the first annual ring in the stem, in the ovulate strobilus, and in the leaf traces of very vigorous leaves of adult trees. In *Sequoia sempervirens* the resin canals were wholly lacking in these regions, but in injured stems and roots of both *S. gigantea* and *S. sempervirens* resin canals were present. In the case of *Sequoia*, then, the presence of resin canals represents a primitive condition in the conifers, retained only in the more conservative regions of the plant in *S. gigantea*, and wholly absent in *S. sempervirens*. A reversion to the ancestral condition in both species may be induced by injury.

According to this later view of the position of the Taxineae as contrasted with that held by PENHALLOW, we have a series of genera starting with *Pinus* as a representative of the most primitive group in which resin canals are normally present, proceeding through *Sequoia* as a type of a group in which resin canals are not normally present in the vegetative axis, until we come to *Podocarpus*, a representative of a group in which resin canals are never present.

In this connection it is important to note that in those groups in which resin canals are normally absent the secretion of resin is carried on by resin parenchyma cells. These resin cells are characteristic of the Taxodineae, Cupressineae, and Podocarpineae. We should expect as the logical outcome of this gradual reduction and simplification of resin secreting structures the final passing out of the resin parenchyma cells in the more modern types. This question will be taken up later when we consider the genera within the group Taxineae.

Much of the controversy in regard to the position of the Taxineae has been based on the character of the gametophytes and reproductive structures, especially the ovulate cone and the method of development of the proembryo. The evidence which I have to offer is derived wholly from the study of the anatomical structure of the stem and root of various genera in the group.

There are included in the family Taxaceae of ENGLER and PRANTL (4) the genera *Phyllocladus*, *Ginkgo*, *Cephalotaxus*, *Torreya*, and *Taxus*. In the most recent classification of the group by COULTER and CHAMBERLAIN (2) *Phyllocladus* is included in the Podocarpineae, *Ginkgo* has been put in a family by itself, and the Taxineae include in addition to *Taxus*, *Torreya*, and *Cephalotaxus*, the doubtful New Caledonian genera *Acmopyle* and *Polypodiopsis*. Turning our attention to the 3 accepted genera of the group, *Cephalotaxus*, *Torreya*, and *Taxus*, I shall attempt to show that the Taxineae are the most modern group of the conifers, that *Cephalotaxus* is the most primitive genus of the subtribe and most nearly related to the Podocarpineae, that *Torreya* is intermediate, and that *Taxus* is the most modern genus of the family and represents, so to speak, the last word in the evolution of the conifers.

If we examine a transverse section of the stem of *Podocarpus totara*, we note the presence in great abundance of resin parenchyma cells (fig. 1). These parenchyma cells are even more evident in the longitudinal section of the stem (fig. 2) as cells which stain densely with haematoxylin due to the presence of resin. These cells are narrower than the tracheids and are characterized by thin walls, by the absence of pits, and end walls at right angles to the long axis of the cell.

A section of the stem of *Cephalotaxus drupacea* (fig. 3) presents a very similar appearance to the stem of *Podocarpus*. That the resin parenchyma cells are widely distributed throughout the annual rings of the stem is evident from a consideration of the low power photograph (fig. 4). The location of these cells is shown by the deep staining of the resinous contents.

The root of *Cephalotaxus drupacea* (fig. 5) shows the presence of resin parenchyma in even greater abundance, and this is the condition we should expect to find, since the root is the more conservative organ of the plant and would retain more fully the primitive or ancestral characteristics of the plant.

The stem of *Torreya taxifolia* presents a very different appearance from the stem of *Podocarpus* and *Cephalotaxus* already considered. Resin parenchyma cells are present throughout the annual ring, but they are much less abundant than in the other stems. The distribution of the cells may be seen in the transverse section (fig. 6), and the character of the cells is shown very clearly in the longitudinal section (fig. 4).

As previously stated, PENHALLOW did not find resin cells in any of the species of *Taxus* or *Torreya* which he investigated, and DEBARY (3) also states that all investigated species of the Coniferae, with the single exception of *Taxus*, have resin passages or resin reservoirs. As a result of my investigation, it is clearly evident that resin parenchyma is present in *Torreya taxifolia*, one of the species investigated by PENHALLOW.

If we examine a transverse section of the stem of *Taxus brevifolia* (fig. 8), we note the complete absence of resin parenchyma cells. A longitudinal section of the same stem (fig. 9) shows even more clearly that the vascular cylinder consists simply of thick-walled tracheids, with numerous bordered pits, and the characteristic spiral thickenings. So far then the condition in *Taxus* tallies with the investigations of PENHALLOW and DEBARY; but if we examine a transverse section of the root of *Taxus cuspidata* (fig. 10) we note the presence of resin parenchyma diffused throughout the annual ring. A higher magnification of a portion of the root is shown in fig. 11. Here the resin parenchyma cells are very conspicuous. A longitudinal view of the same root also shows a view of these parenchyma cells very clearly (fig. 12). The root of *Taxus baccata* also shows the presence of resin parenchyma diffused throughout the annual ring.

Although in the normal stem of the species of *Taxus* investigated there was no resin parenchyma present, a wounded stem of *T. baccata* showed very clearly an extreme development of these cells.

The location of the cells can be determined easily in the transverse section of the stem, due to the fact that the walls stain a deep blue with haematoxylin, and in the longitudinal section the characteristic shape of the parenchyma cells as contrasted with the tracheids make them easily recognizable.

We find then in the normal stem of *Taxus* the condition which we should expect as the ultimate result of the gradual reduction of resin canals, namely, resiniferous parenchyma which finally completely disappears except in the case of conservative organs.

There are three important principles of evolution which have to be considered in working out the ancestry of any group of plants, namely, the principles of recapitulation in the development of the embryo and seedling stages of the plant; retention of ancestral characters in the more conservative regions of the plant, as the root, leaf, and reproductive axis; and reversion to ancestral conditions through injury.

The first of these principles I have not been able to demonstrate, as I did not have access to the seedling stages of the genera investigated. The principle of the retention of ancestral characters in the most conservative organ of the plant is very clearly evidenced in the root of *Taxus cuspidata* by the presence of resin parenchyma cells which have entirely passed out of the stem; and finally the presence in abundance of resin parenchyma in the wounded stem of *Taxus baccata* seems to show clearly that we have in this instance a reversion to the ancestral condition.

From a consideration of these facts the evidence seems to justify the conclusion that the Taxineae are the most modern group of conifers; that of the Taxineae, *Cephalotaxus* is the most primitive, in most nearly resembling *Podocarpus* in the abundance of resin parenchyma; that *Torreya* is the intermediate genus in the group, as shown by the reduction of resin parenchyma, especially in the stem; and that *Taxus* is the most modern genus in the group, since we find here entire absence of resin parenchyma in the stem, although it is retained in the root.

Summary

1. Resin parenchyma is present in abundance in the stem and root of *Cephalotaxus drupacea* and shows clearly its close relationship

to the Podocarpineae, a family in which resin parenchyma is universal.

2. Resin parenchyma is present in less abundance in the stem of *Torreya taxifolia*, showing in this respect an intermediate position between *Cephalotaxus* and *Taxus*.

3. Resin parenchyma is wholly absent in the normal stem of *Taxus brevifolia*, showing that this genus is the most modern one of the group.

4. Resin parenchyma in the root of *Taxus cuspidata* and *T. baccata* and in the wounded stem of *T. baccata* indicates the ancestral condition in this genus.

5. The Taxineae represent a modern group of conifers, as shown by the gradual reduction and final passing out of resin parenchyma in the more progressive organs.

This investigation was carried on in the laboratories of Plant Morphology at Harvard University under the direction of Dr. E. C. JEFFREY, and I wish to express my thanks to him for his invaluable aid in the work and for the many courtesies extended to me during the year spent in his laboratory.

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6. PENHALLOW, D. P., North American gymnosperms. 1907.

EXPLANATION OF PLATES I, II

PLATE I

FIG. 1.—Transverse section of wood of stem of *Podocarpus totara*, ×250.

FIG. 2.—Longitudinal radial section of wood of stem of same, ×250.

FIG. 3.—Transverse section of wood of stem of *Cephalotaxus drupacea*, ×250.

FIG. 4.—Same as fig. 3, ×40.

FIG. 5.—Transverse section of wood of root of *Cephalotaxus drupacea*, ×250.

FIG. 6.—Transverse section of wood of stem of *Torreya taxifolia*, ×250.

PLATE II

FIG. 7.—Longitudinal radial section of wood of stem of *Torreya taxifolia*, ×250.

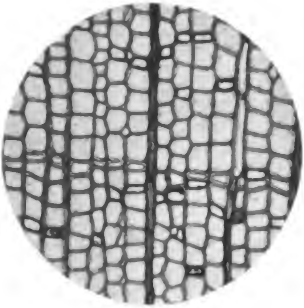
FIG. 8.—Transverse section of wood of stem of *Taxus brevifolia*, ×250.

FIG. 9.—Longitudinal radial section of wood of stem of *Taxus brevifolia*, ×250.

FIG. 10.—Transverse section of wood of root of *Taxus cuspidata*, ×30.

FIG. 11.—Upper portion of same, more highly magnified, ×125.

FIG. 12.—Longitudinal radial section of wood of root of *Taxus cuspidata*, ×125.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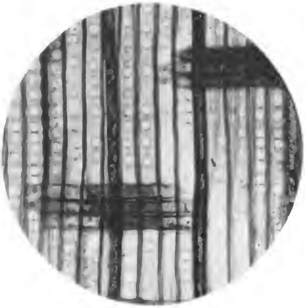
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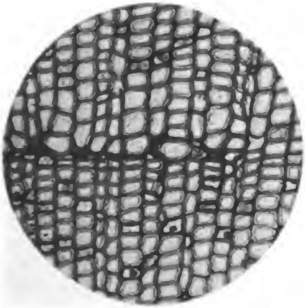
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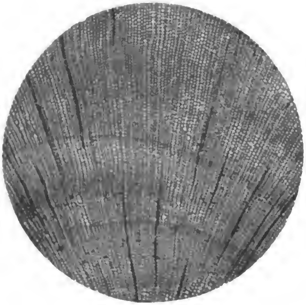
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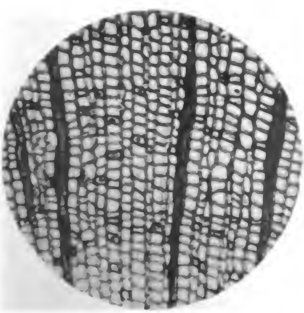
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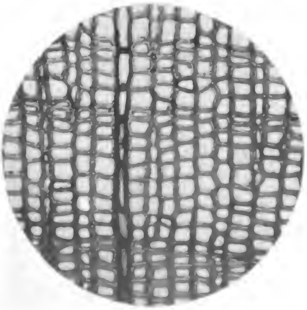
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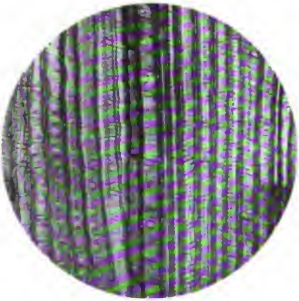
BLISS on TAXINEAE



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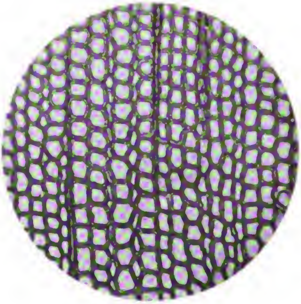

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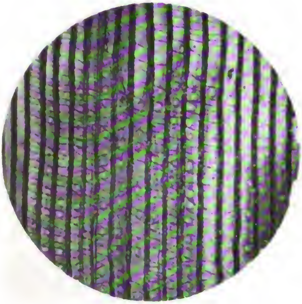

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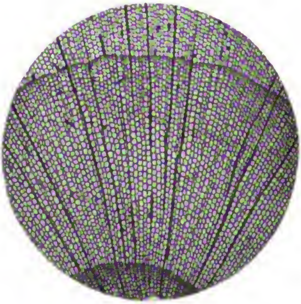

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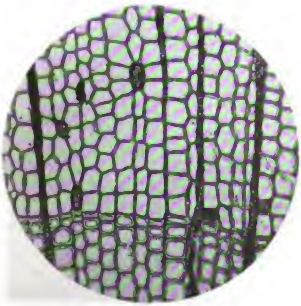

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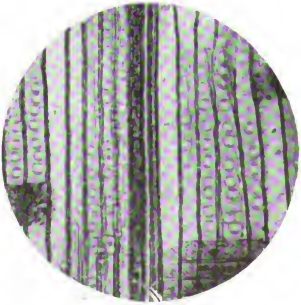

12

BLISS on TAXINEAE

SIGNIFICANCE OF RESINOUS TRACHEIDS

SAMUEL J. RECORD

(WITH FIVE FIGURES)

The occurrence of resinous tracheids in gymnosperms has been noted by PENHALLOW[1] in the woods of certain species of *Cordaites*, *Araucaria*, *Dammara*, and a few representatives of the higher Coniferales, namely, ***Pinus albicaulis***, *P. parviflora*, *Abies Fraseri*, and *A. grandis*. Such tracheids do not differ structurally from other tracheids, but are distinguished by their resinous contents. The resin within them is localized and usually extends across the cavity to form an imperforate septum or plate, which, in unstained sections, may give the cell the appearance of being structurally septate.

PENHALLOW figures the common form of these plates in *Dammara australis*. Figs. 1–3 illustrate the resinous tracheids in the wood of *Pinus albicaulis*, showing the characteristic form of the resin masses (*RPl*) and their association with the medullary rays. The resinous contents of the latter are omitted in order not to obscure the structure. It will be noted that there is considerable difference in the thickness of these plates, which are invariably thinnest in the middle, and not infrequently ruptured there. By comparison with PENHALLOW'S drawings it will be seen that the location, form, and distribution of the resin masses in the two species are identical.

The close association of the rays with the resin plates in the tracheids clearly indicates the origin of the resin, which in some cases can be seen in the form of globules on the outside of the pit membrane of the parenchyma cell. When enough has exuded to form contact with the opposite wall of the tracheid, the surface tension of the liquid and the attraction of the cell wall cause it to assume a double concave form like a drop of water in a small glass tube. Sometimes there is enough resin to fill the tracheid for a considerable portion of its length, at others only enough to produce very delicate plates, while in the case of a cell with a wide lumen the resin may run down along one side or collect in masses without connection across the cavity. It is not unlikely that the presence of gas bubbles in the cells at this stage may play a part in forming the plates and in determining their location, since in some instances a thin plate may be found at a considerable distance from the ray and without visible connection with it.

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[1] PENHALLOW, D. P., A Manual of the North American gymnosperms. Boston: Ginn & Co. 1907 (pp. 53–58).

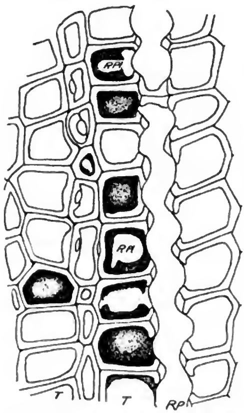

FIG. 1.—Transverse section of *Pinus albicaulis*.

What is the significance of these plates? PENHALLOW says as follows:

> The peculiar form in which the resin is deposited and the particular location of the plates point with much force to their connection with some functional activity, since if it were simply a question of the storage of secreted products, the latter would hardly be disposed as found, but rather after the manner common to so many of the Cupressineae; and this suggestion gains strength from the fact that with respect to the peculiar form of the resin masses as well as their location in the tissue, the Cordaitales are peculiar among the gymnosperms. No exact comparison can be established with other plants, and it is difficult to suggest an adequate explanation. One thing does seem clear, however, and that is that since these plates are of an impervious nature and developed in some cases, at least, in connection with a special constriction of the tracheid cavity, they offer and possibly are specially designed to afford a definite obstruction to circulation in a vertical direction. In this sense they may be designed to serve the same general purpose that is accomplished by the development of tyloses in the vessels of the angiosperms or in the resin passages of the higher Coniferales. It is possible, therefore, that they may be connected in some way, not at present clear, with a more complete restriction of the circulation to a horizontal direction, and particularly through the medium of the medullary rays as specialized channels for that purpose. Among existing

gymnosperms resinous tracheids are almost exclusively confined to *Dammara* and *Araucaria*, though it is a noteworthy fact that similar structures occur rarely among the higher Coniferales. . . . . The taxonomic value of the resinous tracheids applies exclusively to the Cordaitales, where they are of ordinal value, though in *Dammara* and *Araucaria* they may also become of specific value.

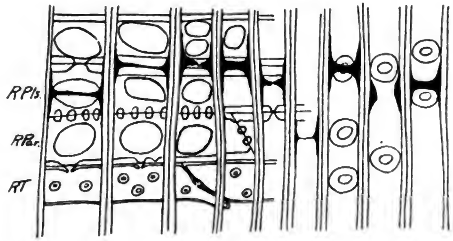

FIG. 2

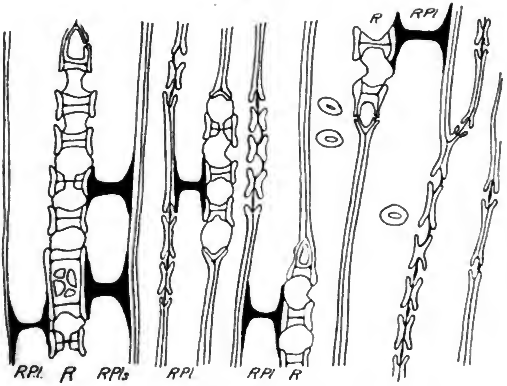

FIG. 3

FIGS. 2, 3.—Fig. 2, radial section; fig. 3, tangential section of *Pinus albicaulis*

The "peculiar form" and the "particular location," upon which PENHALLOW laid special stress, are readily understood when their origin is appreciated. The resin is produced in the parenchyma as a product, or more likely as a by-product, of the metabolic activity of those cells. The cavities of the adjacent tracheids become reservoirs for such portions of the resin as are excreted. Such excretions may retain the form of globules, or extend across the cavity and assume the form of thick or thin plates, or when the quantity is large nearly fill the cell.

The writer does not consider the "Cordaitales" (*Araucarians*) peculiar among the gymnosperms with respect to the form of the resin masses and their location. The same form and location obtain in *Pinus albicaulis*, not sporadically, but as a constant feature of the heartwood. Similar deposits have also been noted occasionally in the tracheids of *P. resinosa*, *Picea sitchensis*, and in abnormal sapwood of *Pinus ponderosa*, while globules of resin have been observed on the outside of the pit membranes of ray parenchyma cells in *P. Strobus*. These instances, taken in connection with PENHALLOW's note of the occurrence of resin plates in *P. parviflora* and in two species of *Abies*, lead the writer to believe that they probably occur sporadically in many other representatives of the Coniferae. The writer has also noted tracheids in *P. albicaulis* with resin globules at several lateral pits connecting with the secondary epithelial cells of a vertical resin duct, showing that resinous tracheids in some instances may be independent of the rays.

The association of the resin plates with special constriction of the tracheid cavity, as noted by PENHALLOW and figured by him for *Dammara australis*, appears to the writer to be without special significance. This constriction is due to increase in thickening of the tracheid walls where in contact with the rays, and has been observed by the writer as a common feature of the woods of various genera of the Coniferae, especially in the thick-walled cells formed late in the season. Such increase is presumably due to greater nutrition at that portion, and in most species is not in connection with resin plates, while the resin masses also occur where there are no such constrictions.

PENHALLOW states that no exact comparison can be established with other plants. The writer believes that exact parallels exist in many of the angiosperms. A good example is *Nyssa sylvatica*, and figs. 4 and 5 show resin-like plates (*RPl*) in this wood which exhibit virtually the same origin, form, and distribution as those in *Pinus albicaulis*. In *Nyssa* these masses occur in both the tracheae and wood prosenchyma and have their origin in the vertical strands of wood parenchyma (*WP*) and in the rays (*R*). Globules (*a*, *b*) are shown emerging from the pits. The plates across the vessels are thin (*c*), but those in the libriform fibers may be very thick (*d*); in fact much of the fiber cavity may be completely

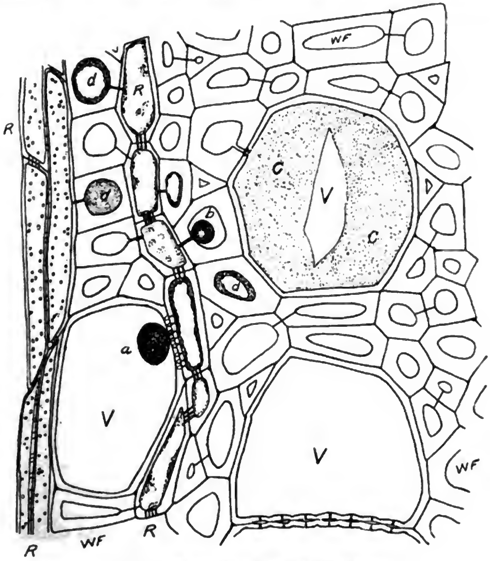

FIG. 4.—Transverse section of *Nyssa sylvatica*

filled except for occasional bubbles. Seen in transverse section a plate in a vessel appears as a thin imperforate membrane thickened in contact with the wall or with a rupture in the middle (fig. 4, *c*), presumably due to shrinkage. Exactly the same features characterize the resin masses in the tracheids of the gymnosperms.

The presence of secretions (or excretions) in the tracheae only or in both tracheae and prosenchyma in the dicotyledons is very common, and in a great many cases such material is in the form of a collar about the cell wall and with a diaphragm of greater or less thickness across the cavity. The writer believes that these various substances, although different in chemical composition, are alike in being excretions resulting from the metabolic activities of parenchyma cells, and represent waste materials. Although produced in varying amount under normal conditions, the greatest production occurs when the cells are about to cease their vital functions and become heartwood, or when a similar condition is produced abnor-

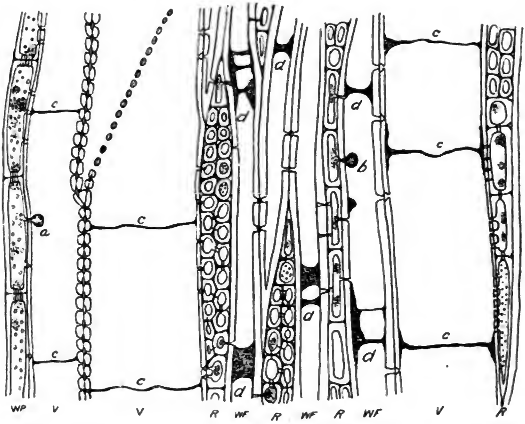

FIG. 5.—Tangential section of *Nyssa sylvatica*

mally, as in severe wounds. The low vitality of the ray and wood parenchyma at that stage may be considered responsible for the excessive amount of waste matter produced, some of which finds its way or is excreted into the cavities of the adjacent cells.

The parallel between the gymnosperms and angiosperms in the manner of their disposal of secreted or excreted products in the xylem extends further. *Pinus*, *Picea*, *Larix*, and *Pseudotsuga*, for example, have vertical resin canals in the wood. Similar canals are normal to the secondary woods of nearly all genera of Dipterocarpaceae and of *Copaifera*, *Daniellia*, *Eperua*, *Kingiodendron*, *Oxystigma*, *Sindora*, and *Prioria* of the Caesalpineoidae. Vertical resin canals arise traumatically in *Abies*, *Sequoia*, *Tsuga heterophylla*, and others; similarly canals may be produced by injury in *Liquidambar*, *Styrax*, *Terminalia*, *Drimycarpus racemosa*, etc. Resin canals in the medullary rays occur normally in *Pinus*, *Picea*, *Pseudotsuga*, and *Larix;* similar canals have been observed by the writer in representatives of 11 genera of Anacardiaceae and 2 of Araliaceae,[2] and others have reported traumatic canals in both planes in *Liquidambar* and *Styrax*.

The writer concludes that resinous tracheids in gymnosperms find numerous parallels in the angiosperms, that they represent one form of reservoir for excretions, and that the form of the resin masses is in response to well known physical laws. No direct functional activity is attributed to the resin plates, although they are in certain ways analogous to tyloses and reduce the permeability of the wood.

As a diagnostic feature resinous tracheids appear of value in *Pinus albicaulis* and may prove to be so in other cases.

YALE UNIVERSITY

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[2] RECORD, SAMUEL J., Intercellular canals in dicotyledonous woods. Jour. Forestry **16**:429–441. 1918.

BRIEFER ARTICLES

BISPORANGIATE CONES OF PINUS MONTANA

(WITH ONE FIGURE)

In the latter part of June 1915 the writer found 3 clusters of bisporangiate cones of *Pinus montana* on a tree along the University Drive, Madison, Wisconsin. Nearly all the cones of each cluster bore both macrosporophylls and microsporophylls, the latter being in every case on the lower portion of the cone. The macrosporophylls were borne in most cases on only the upper portion of the cone. In a few instances the cones were almost wholly staminate or pistillate. The sporophylls and spore sacs appeared to be normal in every respect. No abnormalities were observed in the pollen grains which were stained for a microscopical examination. For the past two years the same tree has failed to produce cones of the type described.

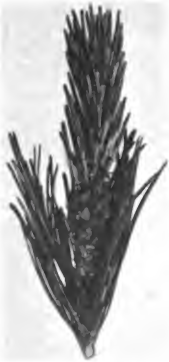

FIG. 1.—Cluster of bisporangiate cones of *Pinus montanum;* darker portion pistillate, lighter portion staminate; reduced one-half.

Bisporangiate cones have been reported in only one other species of pine, namely, in *P. maritima* by GOEBEL (1900). However, in a number of other gymnosperms such cones have been described. More than 50 years ago DICKSON (1860) reported them in *Picea excelsa*, later SHAW (1896) in *Sequoia*, and more recently RENNER (1904) in *Juniperus communis*, and HILL and DE FRAINE (1909) in *Pseudotsuga Douglasii.* In every instance, thus far reported, the microsporophylls and macrosporophylls occupied the same relative positions on the cone as in *Pinus montana.*—W. N. STEIL, *University of Wisconsin, Madison, Wis.*

HEALTHY AND SICK SPECIMENS OF BRYOPHYLLUM CALYCINUM

Those who have worked with *Bryophyllum calycinum*, WALKER, DE VRIES, GOEBEL, the writer, and probably many others, have all noticed that the leaves of *Bryophyllum* which form shoots when isolated will rarely or never do so when in connection with a normal and healthy plant. Miss E. L. BRAUN[1] makes the following statement:

> Pot-grown plants of *B. calycinum* in the writer's possession have frequently grown both shoots and roots from leaf notches while the leaves were in connection with the plant. Early in the spring of 1917 a large plant of *Bryophyllum* began to produce shoots from the leaves more abundantly than the plants often do. The accompanying photographs were taken May 12, when shoot production had reached its maximum. It was not necessary to induce the notches to grow; they grew freely under ordinary room conditions, and with only the usual attention which a pot plant in a residence receives.
>
> A number of the leaves of the plant produced shoots from all the notches or from all except the basal notches, a phenomenon which, to accord with LOEB's theories, should take place only under very special conditions. The plant appears to be a "healthy plant," as healthy and vigorous a plant as the writer has ever seen. Whether or not it is a "normal plant," as a normal plant is conceived of by LOEB, is difficult to say, for nowhere does he define a "normal plant." He does state: "If, however, the flow of substances in a plant is abnormal, either because the roots or the apical parts or both have suffered, a growth of shoots may occur in moist air from the notches of leaves which are in contact with the plant." There is no indication that either the roots or the apical parts have suffered; the plant appears healthy, and has had no accident.

A glance at the photograph accompanying Miss BRAUN's statement will show to those familiar with "normal" *Bryophyllum* that the plant observed and photographed by Miss BRAUN was a sick specimen. The normal stem of *Bryophyllum calycinum* is perfectly straight and vertical (and unbranched). The specimen observed by Miss BRAUN has not a single straight stem. Stems so weak as not to be able to grow vertically upward are certainly abnormal in regard to nutrition. The bend in the stems acts like a partial block to normal circulation. Such sickly bent stems behave to all purposes like isolated pieces of stems whose leaves will in time give rise to shoots.—JACQUES LOEB, *Rockefeller Institute for Medical Research, New York City.*

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[1] BOT. GAZ. **65**: 191. 1918.

CURRENT LITERATURE

NOTES FOR STUDENTS

Hybrid vigor.—The phenomenon of hybrid vigor has come to hold a very important place in practical plant breeding, and is of considerable theoretical interest to geneticists. The most generally accepted interpretation has been EAST'S[1] "heterozygosis," according to which hybrids are vigorous because of their heterozygous sets. Heterozygosis has been very valuable in helping to organize our ideas on the general subject of hybrid vigor, but as a theoretical explanation of the phenomenon involved it has been unsatisfactory. When one says that hybrids are vigorous because of their heterozygous sets, he is making an accurate restatement of the fact of hybrid vigor in the language of genetics, but he is not providing any real explanation of the phenomenon.

The only acceptable "real" explanation that has yet been presented is as follows. In nature a "struggle for existence" occurs among species and individuals. There occurs also a struggle for existence among unit characters. If a unit character is undesirable it is eliminated, since the species possessing it is eliminated. The unit characters, therefore, that have survived and appear in the plants of today are for the most part "desirable" ones, although some undesirable ones also may have survived, having been carried through in association with the "desirable" characters. The majority of unit characters today, however, may certainly be regarded as "desirable" ones, and a majority is sufficient for the present argument.

The question then is raised as to what constitutes a so-called "desirable" character. It may, of course, be any one of a number of things, but is there not some feature common to all such "desirable" characters? The character would seem to be vigor. Each "desirable" character must add somewhat to the vigor of the plant that contains it, and if vigor is increased, such things as size and productiveness will also be increased. Those plants, therefore, will be most vigorous which have in combination the greatest number of "desirable" characters.

The next question is, what plants, in general, have in combination the greatest number of desirable characters? The answer is hybrids, for they combine the "desirable" characters of both parents. Thus, in general, hybrids have twice as many "desirable" characters as do pure races. At this point the objection is raised that though hybrids do actually contain this double quota, each character is represented by only a single dose in the hybrid and by a double dose in the pure race, so that mathematically the two situations are equivalent. This objection is valid only if we assume complete lack of dominance. We are certainly within our rights in assuming some slight degree of dominance, and if we do this it follows that hybrids have more in the way of active "desirable" characters than have pure races, and, having more "desirable" characters, hybrids are more vigorous. They are vigorous, not because they contain more heterozygous sets, but because they contain more positive dominant characters.

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[1] EAST, E. M., and HAYES, H. K., Heterozygosis in evolution and in plant breeding. U.S. Dept. Agric., Bur. Pl. Ind. Bull. no. 243. pp. 58. 1912.

This is a rather obvious explanation of hybrid vigor, and one that has probably occurred to a number of geneticists, being commonly referred to as "the hypothesis of dominance" (accounting for hybrid vigor). It involves 3 assumptions: (1) that there is such a thing as dominance; (2) that most dominant characters are "desirable" ones, that is, of survival value; this assumption is rendered easier if we accept the presence and absence hypothesis; (3) that these dominant "desirable" characters add more vigor than they detract from it, and add to vigor *to the degree in which they are dominant.* This last assumption is the critical one; but even that seems very reasonable.

KEEBLE and PELLEW[2] suggested this explanation in 1910, and since then it has had some discussion in the literature. At first statement the theory seems sound, but actually it does not fit the facts. The two chief objections to this theory of dominance may be found in the publications of SHULL, EMERSON, and EAST (*loc. cit.*).

1. If hybrid vigor were due to dominance, it would be possible in generations subsequent to the F_2 to recombine in one race all of the dominant determiners. Thus there could be isolated a race that was "100 per cent vigorous," and since it would be homozygous, its vigor would not be lost by inbreeding. Actually, though, hybrid vigor cannot be fixed in this way; "all maize varieties lose vigor when inbred."

2. Experience assures us that the distribution of individuals in the F_2 generation with reference to hybrid vigor is represented graphically by a symmetrical curve similar to the normal probabilities curve; the class containing the greatest number of individuals is that which shows the medium amount of hybrid vigor, while on either side of this class the fall in the curve is regular, reaching its lowest point in the two small extreme classes which show respectively greatest hybrid vigor and least hybrid vigor. According to the dominance hypothesis, however, the largest class of F_2 individuals would be that showing the greatest hybrid vigor, while the smallest class would be that showing least hybrid vigor. The curve representing such a situation would be unsymmetrical and strikingly different from that which actually occurs. For these two reasons the dominance hypothesis seems to have been discarded.

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[2] KEEBLE, F., and PELLEW, C., The mode of inheritance of stature and time of flowering of peas (*Pisum sativum*). Jour. Genetics 1:47–56. 1910.

Although it is theoretically attractive, its failure to satisfy these two important details of the hybrid vigor situation has condemned it.

JONES[3] has ingeniously modified the dominance hypothesis so as to avoid these difficulties. At first consideration his theory seems to be clearly the most reasonable explanation of hybrid vigor that has yet been presented, although in time it may encounter destructive criticism. The argument is essentially the same as that for the old dominance hypothesis, with the following important modification. Assume that one parent contains the dominant determiner A, linked with the recessive c; on another chromosome it contains B linked with d. The total formula may be expressed conveniently as Ac, Bd. The other parent has the formula aC, bD. The hybrid is more vigorous than either parent because it combines all 4 dominant determiners. The attractiveness of this scheme is that it escapes the objections that were made to the older dominance hypothesis: (1) the fact that 100 per cent hybrid vigor cannot be fixed is quite in accordance with JONES' scheme, for it is obviously impossible to isolate a homozygous race, combining the 4 dominant determiners, A, B, C, and D (unless crossing over occurs); (2) a simple mathematical demonstration will show that the distribution of F_2 individuals (with respect to hybrid vigor) is quite what it should be, represented by a symmetrical curve, similar to the curve of probabilities. In fact, this new theory, "the dominance of linked factors," seems altogether sound. We should reasonably expect that each chromosome would contain one or more dominant determiners (conducive to vigor) linked with one or more recessives. In this day of factors and determiners such a hypothesis is quite appropriate. It may be, however, that in the future such a phenomenon as hybrid vigor may be explained on the basis of the stabilities and reactivities of the constituents of specific protoplasts.—MERLE C. COULTER.

Taxonomic notes.—BLAKE[4] has published a fascicle of papers containing descriptions of new species. In the paper dealing with Compositae new species are described in *Aphanostephus*, *Diplostephium*, *Verbesina*, *Liabum*, and *Cirsium*. Collections from Venezuela and Curaçao contain new species in the following genera: *Ruprechtia* (2), *Atriplex*, *Bauhinia*, *Croton* (2), *Maytenus*, *Zizyphus*, *Vismia*, *Hecatostemon* (a new genus of Flacourtiaceae), *Passiflora*, *Jacquinia*, *Bumelia*, *Aspidosperma*, *Plumeria*, *Marsdenia* (2), *Lycium*, *Tabebuia*, *Dianthera*, *Oxycarpha* (a new genus of Compositae), *Simsia*, and *Verbesina*. The new species from Oaxaca are referred to *Iresine* (2), *Amyris*, *Guarea*, *Tri-*

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[3] JONES, D. F., Dominance of linked factors and heterosis. Genetics 2:466–479. 1917.

[4] BLAKE, S. F., II. Further new or noteworthy Compositae. Contrib. Gray Herb. N.S. no. 53. pp. 23–30. 1918.

———, New Spermatophytes collected in Venezuela and Curaçao by Messrs. Curran and Haman. *Ibid.* pp. 30–55.

———, New plants from Oaxaca. *Ibid.* pp. 55–65.

chilia, *Comocladia*, *Astronium*, *Myginda*, *Homalium*, *Schismocarpus* (a new genus of Loasaceae), *Cuphea*, *Ardisia*, and *Bouvardia*.

BRITTON[5] has described a new *Scirpus* (*S. Congdoni*) from California, which is the species from the Pacific states heretofore called *S. atrovirens*.

Miss BURLINGHAM[6] has described 4 new species of *Russula* from Massachusetts.

FARWELL[7] has described 17 new varieties of Michigan plants, distributed among 9 families; and has also published a list of rare or interesting plants from the state.

FERNALD[8] has described a new species of *Littorella* (*L. americana*), one of our rarest plants, and heretofore referred to the European *L. uniflora*. The same author,[9] as a result of his study of *Epilobium* from various regions, has published a number of new varieties and combinations and discussed several critical forms.

GREENMAN,[10] in continuation of his monograph of *Senecio*, has presented TOMENTOSI, recognizing 35 species, 2 of which are new, occurring in California and Colorado. The descriptions are accompanied by a full bibliography and liberal citations of exsiccatae, especially such as occur in American herbaria.

JOHNSTON and BRUNER[11] have described a new species of *Phyllachora* (*P. Roystoneae*) found on the leaves of the royal palm (*Roystonea regia*) growing in Cuba. It is described as forming "conspicuous black, carbonaceous masses several centimeters long on the midribs of the leaves."

MACBRIDE[12] has described new species in *Tricyrtis*, *Atriplex*, *Lotus*, *Lomatium*, *Lycium*, and *Cirsium*, and presented the results of his studies of numerous other forms.

MURRILL,[13] in continuation of his studies of the Agaricaceae of tropical North America, has begun the presentation of the subtribe Agaricanae, recognizing 14 species, 6 of which are included in the present contribution. New species are described in *Atylospora* (11), *Psathyrella* (5), *Psilocybe*, and *Campanularius*. In a later paper the same author[14] has described 28 new species from the same region in the following genera: *Drosophila* (8), *Hypholoma*, *Gomphidius*, *Stropharia* (2), *Agaricus* (13), *Coprinus* (4).

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[5] BRITTON, N. L., An undescribed *Scirpus* from California. Torreya **18**:36. *fig. 1*. 1918.

[6] BURLINGHAM, GERTRUDE S., New species of *Russula* from Massachusetts. Mycologia **10**:93–96. 1918.

[7] FARWELL, O. A., New species and varieties from Michigan. Mich. Acad. Sci. Rep. 1917. pp. 247–262.

[8] FERNALD, M. L., The North American *Littorella*. Rhodora **20**:61, 62. 1918.

[9] ———, *Epilobium*, etc. Rhodora **20**:1–10, 29–39. 1918.

[10] GREENMAN, J. M., Monograph of the North and Central American species of the genus *Senecio*. Part II. Ann. Mo. Bot. Gard. **5**:37–108. *pls. 4–6*. 1918.

[11] JOHNSTON, J. R., and BRUNER, S. C., A *Phyllachora* of the royal palm. Mycologia **10**:43, 44. *pl. 2*. 1918.

[12] MACBRIDE, J. FRANCIS, New or otherwise interesting plants, mostly North American Liliaceae and Chenopodiaceae. Contrb. Gray Herb. N.S. no. 53. pp. 1–22. 1918.

[13] MURRILL, WILLIAM A., The Agaricaceae of tropical North America. VII. Mycologia **10**:15–35. 1918.

MILLSPAUGH and SHERFF[15] have discovered that the species of *Xanthium* are in great confusion, and have described 5 new species, from Vermont (*X. leptocarpum*), New York (*X. arcuatum*), North Carolina (*X. cylindricum*), and Texas (*X. crassifolium* and *X. acutilobum*). In the same paper a new species of *Solidago* (*S. emarginata*) from Illinois is described.

SMITH and SMALL[16] have described a new genus (*Cavea*) of Compositae from India, in the East Himalaya region, belonging to the Inuloideae. It is an extreme alpine form, its structure associating it with *Pluchea*, but its appearance suggesting *Saussurea* or *Berardia*.

STEPHANI,[17] in continuation of his *Species Hepaticarum*, has completed *Metzgeria* and presented 25 other genera, ending with *Plagiochila*. A new genus (*Kormickia*) is described and 121 new species distributed among 9 genera. The largest genus is *Plagiochila* with 187 species, 92 of which are new. The remaining 29 new species are distributed among the following genera: *Metzgeria* (11), *Symphyogyna* (3), *Funicularia*, *Solenostoma*, *Jungermannia* (2), *Jamesoniella* (6), *Anastrophyllum* (3), *Lophozia* (2).

WALTON[18] has described a new genus (*Eutetramorus*) of algae secured from the plankton of a pond on the campus of Ohio State University at Columbus. It belongs to the Coelastraceae (Protococcoideae), the colony consisting of 16 cells.

ZELLER and DODGE[19] have monographed the genus *Rhizopogon* in North America, recognizing 12 species, 6 of which are described as new. In addition, 15 species are presented which have not as yet been found in North America, but may be discovered later. Among these "extra-limital" species 2 are described as new.—J. M. C.

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[14] MURRILL, WILLIAM A., The Agaricaceae of tropical North America. VIII. Mycologia **10**:62–85. 1918.

[15] MILLSPAUGH, C. F., and SHERFF, E. E., New species of *Xanthium* and *Solidago*. Publ. Field Mus. Nat. Hist. **4**:1–7. *pls. 1–6*. 1918.

[16] SMITH, W. W., and SMALL, JAMES, *Cavea*, a new genus of the Compositae from the East Himalaya. Trans. and Proc. Bot. Soc. Edinburgh **27**:119–123. *pl. 5*. 1917.

[17] STEPHANI, FRANZ, Species *Hepaticarum* **6**:49–176. 1917. 1918.

[18] WALTON, L. B., *Eutetramorus globosus*, a new genus and species of algae belonging to the Protococcoidea. Ohio Jour. Sci. **18**:126–128. 1918.

[19] ZELLER, SANFORD M., and DODGE, CARROLL W., *Rhizopogon* in North America. Ann. Mo. Bot. Gard. **5**:1–30. *pls. 1–3*. 1918.

Abscission.—HODGSON[20] and KENDALL[21] have recently contributed to the literature on the abscission problem, the former having investigated foliar abscission in *Citrus* and the latter the abscission of flowers and fruits in 10 genera of the Solanaceae, and particularly in *Nicotiana*. The investigation of an abscission problem may be expected to resolve itself into an effort to determine the following points: (1) the histology of the tissue in which the abscission takes place, and the position of the abscission zone therein; (2) the extent of the abscission zone, its histological differentiation, if any, and its development, that is, whether performed or not; (3) the position of the separation layer within the abscission zone, and the nature of the actual abscission process, that is, the method of cell separation; (4) the time of abscission, involving both reaction time and abscission time; and (5) the possibility of inducing abscission experimentally (by poisonous gases, mechanical injury, etc.). The most vital as well as, often, the most obscure of these matters which should receive consideration is the one involving the determination of the method of cell separation. In this connection both HODGSON and KENDALL found, in the species investigated, that the abscission process conforms to the usual type which involves the separation of cells along the plane of the middle lamella. No cell divisions or elongations were observed to precede or accompany abscission. HODGSON notes a remarkable swelling and gelatinization of the cell walls of the separation layer, which is followed by a dissolution of the gelatinized walls. In this case such cells, after functioning in abscission, resume growth and divide rapidly for a time. The abscission problem in *Citrus* is of peculiar interest because of the well known shedding of immature oranges of the Washington navel variety which annually results in considerable financial loss to orange growers.[22]

KENDALL's article contains a more or less satisfactory consideration of all these points noted as of interest, but, as is perhaps inevitable in an attempt to cover so wide a field, no more than a beginning is made in working out some of the more fundamental problems. Thus, he shows that from water extracts of separation zones in which abscission has commenced a decidedly heavier precipitate comes down in 95 per cent alcohol than from those in which abscission has not started. This difference is tentatively ascribed to the presence of pectin in the first case, it being derived from the hydrolysis of pectose during the dissolution of the primary cell membranes in the activated separation cells. This conclusion may or may not be justified, but such experiments indicate lines along which future investigation should lie, especially in view of the fact that KENDALL succeeded with lower percentages of alcohol in bringing down a different type of precipitate. This latter precipitate might be expected to yield cytolytic enzymes. He also finds a reduction in the sugar content of abscission zones following cell separation, and that the normal acidity on *Nicotiana* pedicels is low and is only slightly reduced during abscission. This latter fact is taken to indicate that the activity of enzymes alone is responsible for the dissolution of the middle lamellae during cell separation.

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[20] HODGSON, R. W., An account of the mode of foliar abscission in *Citrus*. Univ. Calif. Publ. Bot. **6**:417–428. 1918.

[21] KENDALL, J. N., Abscission of flowers and fruits in the Solanaceae with special reference to *Nicotiana*. *Ibid*. **5**:347–428. 1918.

[22] HODGSON, R. W., Some abnormal water relations in citrus trees of the arid Southwest and their possible significance. Univ. Calif. Publ. Agr. Sci. **3**:37–54.

KENDALL reports that illuminating gas and laboratory air will cause abscission in the majority of the species investigated, but that resistance to abscission stimulated in this manner appears suddenly in some species. Tests were also made as to the effect of a variety of mutilations of the flower and pedicel in inducing abscission. Relatively slight injuries to the ovary were effective, whereas considerable amounts of tissue had to be removed in the case of other flower parts before abscission was induced. It is interesting to note that mechanical injury was not found to be particularly effective in the tomato, and that the following species rarely or never exhibit floral abscission: *Nicotiana Bigelovii* (3 varieties), *N. quadrivalvis* (2 varieties), *N. multivalvis, Petunia hybrida, Salpiglossis sinuata, Salpichora rhomboidea*, and *Lycium australis*. A detailed summary of the pertinent literature is included in KENDALL'S paper. —T. H. GOODSPEED.

Nitrates in forest soils and forest regeneration.—In an important contribution HESSELMAN[23] has reviewed the present state of our knowledge of the composition of forest soils and finds, among other things, that while from earth containing relatively little humus it has been possible to isolate organic compounds of known composition the humus of many soils is composed largely of chemical compounds of undetermined character, but that on the whole the constituents are colloidal in nature and are largely influenced by the amount of mineral salts in the soil and ground water. He distinguishes two types of forest humus soils, the "mild humus" characteristic of deciduous forests, well aerated and containing nitrate-forming as well as denitrifying bacteria, and "raw humus" found in coniferous forests as a series of layers of leaves and litter in various stages of decomposition from which nitrate-forming and denitrifying bacteria are usually absent.

Recognizing decomposing litter as one of the principal sources of nitrogen in forest soils, he has investigated the "decay capacity" of various forest types, using several different methods. He has determined the relative abundance of various bacteria, the nitrogen content of trees and plants, and has shown that nitrate supply and nitrate formation is at its maximum in beech forests and at its minimum in mossy coniferous stands. Lime in the soil and in solution in the ground water tends to promote nitrification. He points out that by proper forest management the formation of nitrates may be accelerated and a decided increase in timber production obtained.

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[23] HESSELMAN, HENRIK, Studier över saltpeterbildningen i naturliga jordmåner och dess betydelse i växteekologiskt avseende (with abstract in German). Meddel. från Statens Skogsförsöksanst. Haft. 13–14. 297–527. *pls. 7. figs. 30.* 1917.

In a second article[24] he investigates the problems of the regeneration of conifer forests, with particular reference to the transformation of nitrogen, for it appears that while trees of pine and spruce often grow in forests where no nitrate formation is taking place, the raw humus developed beneath their dense shade does not prove a good soil for the rapid growth of their seedlings. It seems from experimental evidence that nitrogen transformation in such soils may be initiated and accelerated by the introduction of light through cutting, by burning the surface, or by stirring the surface soil. Decaying timber seems to favor nitrogen transformation, and this may tend to account for the observed abundance of conifer seedlings growing upon fallen logs.

In mixed conifer stands, especially where the herbaceous undergrowth is good, nitrate formation is, in contrast, rather active; so much so in many instances as to induce such a rank growth of herb and grass vegetation in clearings as to crowd out conifer seedlings. These and other data should help to explain to the ecologist many phenomena of secondary succession, while from the same data the forester should receive guidance for the formulation of a policy of forest management that will favor the formation of the amount of nitrogen best suited to the regeneration of the forest.

The value of these excellent papers is increased by an abundance of tabulated data, by being freely illustrated, and by extensive bibliographies.—GEO. D. FULLER.

Mechanics of movement in insectivorous plants.—Two recent papers on this subject, by BROWN[25] and by HOOKER,[26] have supplied some interesting information. Although different plants were used, the results are comparable in many respects. Both investigators find that the bending is accompanied by an extension of the cells on the convex side, which soon becomes fixed by growth; that there is little or no change of size in the cells of the concave side; and that unbending is accompanied by growth on the concave side. HOOKER finds the osmotic pressure of the cells on the convex side of bending tentacles less than that on the concave side, and this decrease is proportional to the increase in the length of the cells. He finds no changes in permeability and concludes that the increased size of the cells is due to decreased elasticity of the cell walls.

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[24] HESSELMAN, HENRIK, Om våra skogsföryngringsåtgärders inverkan på saltpeterbildningen i marken och dess betydelse för barrskogens föryngring (with abstract in English). Meddel. från Statens Skrogsforsöksanst. Haft 13–14. 923–1076. *pls. 15. figs. 48.* 1917.

[25] BROWN, WM. H., The mechanism of movement and the duration of the effect of stimulation in the leaves of *Dionaea*. Amer. Jour. Bot. 3:68–90. 1916.

[26] HOOKER, HENRY D., JR., Mechanics of movement in *Drosera rotundifolia*. Bull. Torr. Bot. Club **44**:389–403. 1917.

BROWN reports no determinations of osmotic pressure, but finds that if closed leaves of *Dionaea* are killed, before the extension of the cells has become fixed, and passed through alcohol to xylene, the leaves reopen, and close again when passed back through alcohol to water. He concludes that the increase in size of the cells is due to increased osmotic pressure. He believes there is no permeability change, and thinks changes in the elasticity of the cell walls improbable. It is interesting if, in fact, the mechanics of these two responses, so similar in many respects, are so widely different in another.

Geotropic bending of growing organs is similar in many respects to the movements studied. Its comparative slowness should make it somewhat easier to follow, and the results might furnish valuable suggestions as to the mechanics of these more rapid movements. SMALL[27] has found differences in permeability in the two flanks of *Vicia Faba*, roots bending geotropically.—THOMAS G. PHILLIPS.

Soil moisture studies.—The extensive investigations of BRIGGS and SHANTZ have shown the importance of the moisture equivalent as a constant that will measure the physical properties of soils. Two recent studies deal with certain phases of the same phenomena. The first[28] shows that while the addition of various salts does not materially change the moisture equivalent of the soil under investigation, if the same salts are washed from the soil with water it then seems to possess a new and peculiar set of physical properties and its moisture equivalent is markedly increased. This increase varies from 2 to 40 per cent, and is taken to mean that the washing out of the salt has increased the interior surface of the soil.

The second article, by SMITH,[29] reports the investigation of the relationship between the results of mechanical analysis and the moisture equivalent. He concludes that there is at present no formula that gives more than a rough approximation of this relationship, and hence that the moisture equivalent cannot be indirectly determined by mechanical analysis with any degree of accuracy.—GEO. D. FULLER.

Soil aeration and root growth.—Roots of various plants appear, according to the results of CANNON and FREE,[30] to respond quite differently to variations in the composition of the soil atmosphere, and this difference in response seems to be related to the character of the natural habitat of the species in question. Thus *Salix* sp. (probably *nigra*) stands at one end of the series and shows no injurious effect even when the oxygen of the atmosphere is entirely replaced by either nitrogen or carbon dioxide. At the opposite end of the series stands *Opuntia versicolor*, growth of roots ceasing with an atmosphere containing 50 per cent carbon dioxide, while *Coleus Blumei* is comparable to it, showing injury and ultimate death with the addition of 25 per cent nitrogen to the soil atmosphere. Of the other species tested *Heliotropium peruvianum* was closely comparable to *Opuntia*, while *Nerium oleander* and *Prosopis velutina* prove nearly as resistant as *Salix*. The results seem to indicate that plants growing naturally in well drained soil are much more sensitive to the composition of the soil atmosphere than those from swamps and poorly drained habitats.—GEO. D. FULLER.

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[27] SMALL, JAMES, Geotropism and the Weber-Fechner law. Ann. Botany **31**:313–314. 1917.

[28] SHARP, L. T., and WAYNICK, D. D., The moisture equivalent determinations of salt-treated soils and their relation to changes in the interior surfaces. Soil Sci. **4**:463–469. 1917.

[29] SMITH, ALFRED, Relation of the mechanical analysis to the moisture equivalent of soils. Soil Sci. **4**:471–476. 1917.

[30] CANNON, W. A., and FREE, E. E., The ecological significance of soil aeration. Science, N.S. **45**:178–180. 1917.

Embryo of Aucuba.—PALM and RUTGERS[31] have settled the question of apogamy in *Aucuba japonica*, which has been under suspicion for 40 years. They bagged 300 pistillate flowers and not a single fruit formed, while 600 isolated pistillate flowers produced normal fruit after artificial pollination. It is thought that EICHLER's original suggestion of apogamy probably came from the fruiting of an isolated pistillate plant which had developed staminate flowers, since the authors have repeatedly found staminate flowers on pistillate plants. Staminate plants have also been observed to produce pistillate flowers.

The flowers open about the time of megaspore formation, and the embryo sac reaches the fertilization stage about 4 weeks later. The solitary megaspore mother cell becomes deeply placed by the extensive development of parietal tissue. The behavior of the 4 megaspores is usually quite normal, but in one case the 2 megaspores nearest the chalaza were found in division. The development of the gametophyte is normal, but stages in endosperm formation were not obtained. The chromosome numbers were determined to be 18 and 36. —J. M. C.

Disease resistance.—JONES[32] has published a summary of his results in securing a race of cabbage resistant to the "yellows." Some of the fundamental questions involved in resistance were considered. The difference between susceptible and resistant plants was found not to be due to any superficial obstacle, but to the different relations of the interior cells of the host and parasite. "The resistant tissues have the ability to restrain the development of the parasite to a greater degree than do the susceptible and so give time for protective cork formation." It was shown also that resistance is clearly inheritable, not as a single character, but as a complex of a number of heritable factors. Environmental factors were found to have a marked influence upon invasion by the parasite (***Fusarium***), there being a "critical soil temperature" (about 17° C.) for such invasion. Below this the plants are not invaded even in the sickest soils.—J. M. C.

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[31] PALM, BJ., and RUTGERS, A. A. L., The embryology of *Aucuba japonica*. Rec. Trav. Bot. Néerland. **14**:119–126. *figs. 12.* 1917.

[32] JONES, L. R., Disease resistance in cabbage. Proc. Nat. Acad. Sci. **4**:42–46. 1918.

Desiccation.—An investigation of the course of desiccation and partial starvation in cacti has been made by MACDOUGAL, LONG, and BROWN.[33] The principal studies center upon the changing rate of water loss, chemical changes in the food reserves, plasmatic colloids and cell sap, and the morphological changes which occur during long periods of desiccation. In one case a large *Echinocactus* was under observation for 6 years after removal of the plant from the soil. Water loss is rather rapid at first, but proceeds more and more slowly with time. While 10 per cent of the water was lost the first year in one specimen, during the sixth year only 5 per cent of the water remaining at the beginning of that year was lost. The loss of water is much more rapid of course in the open than in diffuse light, and *Echinocactus* can withstand desiccation not more than 2 years with free exposure.—GEO. D. FULLER.

Aeration of nutrient solutions.—STILES and JÖRGENSEN[34] find that aeration of the nutrient solution increases the rate of growth of barley, as found by various workers, but has no effect on the growth of buckwheat, as found by FREE. They carefully limit their conclusion to the condition under which they experimented, and find themselves unable to explain this specific difference. They emphasize the necessity of knowing much more about the physical chemistry of water culture solutions. They also feel that neither the law of the minimum nor the principle of limiting factors gives an adequate expression of the behavior of the plant as a whole.—WM. CROCKER.

Apogamy in ferns.—STEIL[35] has discovered apogamy in a large number of ferns, the investigation extending over a period of 6 years. It seems that apogamy is of frequent occurrence in *Pellaea*, *Pteris*, and *Aspidium*. The prothallia were grown under cultural conditions favorable for the development of sex organs and embryos in non-apogamous species. Many interesting details of embryo development are given, which much extend our knowledge of this phenomenon.—J. M. C.

---

[33] MACDOUGAL, D. T., LONG, E. R., and BROWN, J. G., End results of desiccation and respiration in succulent plants. Physiol. Res. **1**:289–325. 1915.

[34] STILES, W., and JÖRGENSEN, I., Observations on the influence of aeration of the nutrient solution in water culture experiments, with some remarks on the water culture methods. New Phytol. **16**:182–197. 1917.

[35] STEIL, W. N., Studies of some new cases of apogamy in ferns. Bull. Torr. Bot. Club **45**:93–108. *pls. 4, 5.* 1918.

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THE
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AUGUST 1918

DETERMINATION OF WILTING

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 241

ARTHUR L. BAKKE

(WITH FIVE FIGURES)

The status of the question of permanent wilting in plants, as described by BRIGGS and SHANTZ (**5, 6, 7, 8**), CALDWELL (**11**), SHIVE and LIVINGSTON (**37**), and ALWAY (**1**), centers about the determination made by BRIGGS and SHANTZ that a plant is regarded as having attained a condition of permanent wilting when it does not recover its turgidity in a period of 24 hours when surrounded by air saturated with water vapor. The method of employing standardized hygrometric paper (**2, 3, 4, 28, 30, 38, 40, 42**) in the measurement of the transpiring power in plants consists in ascertaining the power of a leaf to give off water and comparing this with the power represented by a saturated blotting paper surface at the same time. This is then a measure in both cases of the resistance to the passage of water. The conditions which affect such measurements are internal, but these internal factors are dependent upon external factors. It is obvious, therefore, that data derived will be more or less of a resultant complex of all the forces which have been operative during the history of the plant.

The method in principle is the same as has previously been used in investigations upon the foliar transpiring power of plants. In the present studies filter paper circles (Munktell's Swedish no. 00—11 cm.)[1] are impregnated with 3 per cent solution of cobalt chloride and are later cut into small squares. Just before using, these squares are heated over a bicycle lamp, or on a granite pie-plate suspended by a clamp over the flame of an alcohol lamp, until they become blue. One of these squares is placed between the jaws of a "transpiration clip," and as quickly as possible applied to either the upper or lower surface of a leaf. The time required to change the paper square from blue to pink is determined in seconds. The time which it takes to change a similar piece of cobalt paper from blue to pink when placed over a moist blotting paper surface blanketed by a millimeter of air (**2, 4, 28, 30, 34, 42**) is recorded. The water apparatus is the same as used by BAKKE and LIVINGSTON (**4**). TRELEASE and LIVINGSTON (**42**) have developed the relations of the temperature to vapor tension as first shown by BAKKE (**2**). These authors have presented a formula whereby the time interval may be ascertained on knowing the temperature. LIVINGSTON and SHREVE (**30**) have recently improved and modified this method. The principal improvement is in the adoption of permanent color standards. Instead of the simple square of cobalt chloride paper, a composite slip is employed consisting of a small piece of the hygrometric paper in juxtaposition with two slips having permanent color standards. These provide both an initial and an end point for the color change. For use in the laboratory they advocate and describe a simpler form of standard water evaporating apparatus. These modifications were not used in this study.

The possibilities of using the original method of standardized hygrometric paper in determining the extent of wilting and the permanent wilting point was first suggested to me by its author, B. E. LIVINGSTON, at the Desert Laboratory of the Carnegie Institution during the summer of 1913. In 1914 the writer (**3**), working at the Desert Laboratory, performed a series of measurements upon sunflower plants lifted from the soil and later brought into the laboratory to wilt. The results of this series of tests show that wilting occurs at a definite point and that permanent wilting represents the most intense wilting possible, without serious rupture of the water columns of the plant. These studies have been amplified in the present investigation. The experimentation involved in the present study was performed in the greenhouse of the University of Chicago during the summers of 1915 and 1916. The large Russian variety of the common sunflower (*Helianthus annuus*) was used, the seed being from W. W. BARNARD of Chicago. The experiments involving the porometer were performed in the laboratory of Plant Physiology of Iowa State College. The plants were the same variety, but seed was secured from the Iowa Seed Company of Des Moines, Iowa.

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[1] LIVINGSTON and SHREVE in a more recent publication (Improvements in the method for determining the transpiring power of plant surfaces by hygrometric paper. Plant World **19**: 287–309. 1916) have recommended Whatman's filter no. 30 (11 cms.) circles as being superior to the Swedish paper.

Series of 1915

METHOD

The seeds used in the tests for 1915 were planted in sheet iron containers 6×6 inches, on June 31. Germination was forced by placing the containers in a warm house. When the cotyledons had made their appearance, the seedlings were thinned out so that only 3 remained. The cultures were then removed to a cooler place, where the plants were allowed to grow until they were approximately 6 weeks old and about 40 cm. high. The soil used in this series consisted of 4 parts of compost and 1 part sand. The water-holding capacity was calculated to be 47 per cent. The plants remained in the same containers throughout the entire period of the experiment. They were watered from time to time until the morning of July 13, when they were heavily watered, and after that no more water was added until the morning of July 16, when the plants were lightly watered and the soil surface covered with plasticine. Two plants were used as checks in testing out wilting by the BRIGGS and SHANTZ method.

The values for the indices of foliar transpiring power were obtained according to the original Livingston method; the standard water apparatus was the same as described by BAKKE and LIVINGSTON. Throughout the series, cobalt paper squares made from Munktell's Swedish no. 00 filter paper were used. As the work was carried on in the greenhouse, the usual bicycle lamp for lighting was replaced by electric light. The cobalt paper squares were warmed upon a granite pie-plate, which was adjusted by a clamp over an alcohol flame, so that the paper squares were heated to a temperature sufficient to give them the blue color.

EXPERIMENTATION

The readings for the 1915 series, begun on August 16, were usually made between the 10th and 11th hours and again between the 20th and 21st hours. Two plants were used for the foliar transpiring power tests; two additional plants were used for the wilting determinations according to the method of BRIGGS and SHANTZ. Evaporation was determined at the same time by a standardized Livingston form of cylindrical atmometer. The readings as recorded in table I show the maximum foliar transpiring power as occurring about the 11th hour, while the minimum usually occurs after sunset. Wherever possible, leaves of different ages were used and were numbered and tagged Ia_1, Ia_2, Ia_3, Ib_1, Ib_2, etc., the highest number representing the youngest leaf. In this way the same leaf could be used throughout.

The average results of the foliar transpiring power indices, as represented graphically (fig. 1), show a general decline from August 16 to August 20. The maximum index reached on August 17 possesses a value of 0.89. This index is almost the same as the one obtained earlier by BAKKE and LIVINGSTON. Although the plants were watered a little on the day the experiment was begun, they must have given off considerable water during the previous 3-day interval. That the soil moisture content has an appreciable effect upon foliar transpiring power has been proven previously, and from the nature of transpiration it is self-evident. The *Helianthus* plants of BAKKE and LIVINGSTON were growing in a place where the soil moisture was less than would be regarded as optimum. In all probability the two sets of *Helianthus* plants were grown in soil having practically the same amount of moisture. The soil moisture content in both series was below the amount necessary for the production of the greatest growth.

For the first half of the series the highest transpiring power occurs during the day, while the lowest transpiring power values are at night. The average day values are accordingly 0.72, 0.92, 0.74, 0.38, 0.26, 0.19, 0.32 for one set (I*a*); for the other (I*b*), 0.61, 0.89, 0.76, 0.30, 0.30, 0.39, 0.42. The average night values for the first series are 0.29, 0.34, 0.24, 0.19, 0.25, 0.44, 0.69; for the second series, 0.31, 0.39, 0.23, 0.16, 0.50, 0.45, 0.61. The results obtained by calculating the ratio of the respective day and night values are rather uniform. For August 16 the average ratio is 2.4; for August 17, 2.7; the remaining values for I*a* are 3.1, 2.0, 1.0, 0.43, 0.46. The corresponding respective values for series I*b* are 2.0, 2.3, 3.3, 1.9, 0.77, 0.87, 0.61. For the first two days, August 16 and 17, the probable normal ratio is between 2 and 3. On the following day there is a slight increase, and after that there is a decrease. Whether the rise in the ratio on the third day presents a normal situation or not cannot at present be stated; at any rate the value is not far from 3. The decrease in foliar transpiring power after August 19 and the resulting decrease in the ratio do not show any definite mathematical relation. For a plant growing in a normal environment, a rise in evaporation will give an increase in transpiring power, but on August 22 there is a high evaporation, a low foliar transpiring power, and a lower day value than night value. Such a status must be looked upon as abnormal for growing plants. Beginning with August 21 there is a rapid ascent.

Considerable agreement is present between the graphs in this series and the one for *Helianthus* (3), where the plants were lifted from the soil. There is a decrease in the foliar transpiring power to a point where there is more or less of a balance, and then again where there is an increase. The time element in the present series is extended over a longer period, and as a result variations which might be masked in the series of short duration would be present.

The rupture of the water columns of the plants of the 1915 series is as definite as that presented for the plants lifted from the soil in southern Arizona. The outstanding feature of the curve is the very marked rise on August 20. Upon examination of the rate of evaporation, it will be at once evident that the evaporating power of the air was very low throughout. Two plants of this

TABLE I

INDICES OF FOLIAR TRANSPIRING POWER FOR 3 DIFFERENT LEAVES OF TWO *Helianthus* PLANTS DURING PROGRESSIVE MARCH OF WILTING FROM AUGUST 16–22, 1915 (MAXIMA IN BOLD FACED TYPE, MINIMA IN ITALICS)

LEAF NUMBER	DAY AND HOUR OF OBSERVATION	INDEX OF TRANSPIRING POWER			EVAPORATION FROM STANDARDIZED ATMOMETER, CC. PER HOUR	DAY AND HOUR OF OBSERVATION	INDEX OF TRANSPIRING POWER			EVAPORATION FROM STANDARDIZED ATMOMETER, CC. PER HOUR	RELATION OF DAY TO NIGHT
		Lower	Upper	Entire			Lower	Upper	Entire		
Ia$_1$	August 16 11:00	0.64	0.49	0.56	....	August 16 20:00	0.27	0.18	0.23	0.45	2.4
Ia$_2$		0.94	0.52	0.73			0.36	0.23	0.30		2.4
Ia$_3$		0.98	0.74	0.86			0.41	0.27	0.34		2.5
		Average 0.85	0.58	0.72			0.35	0.23	0.29		2.4
Ib$_1$	11:00	0.74	0.36	0.55			0.41	0.19	0.30		1.8
Ib$_2$		0.94	0.39	0.67			0.40	0.22	0.31		2.2
		Average 0.84	0.38	0.61			0.41	0.21	0.31		2.0
Ia$_1$	August 17 10:00	0.89	0.80	0.85	0.40	August 17 21:00	0.39	0.20	0.30	0.17	2.8
Ia$_2$		0.94	0.94	0.94			0.42	0.24	0.33		2.8
Ia$_3$		0.97	0.97	0.97			0.48	0.32	0.40		2.4
		Average **0.93**	**0.90**	**0.92**			0.43	0.25	0.34		2.7
Ib$_1$		0.97	0.64	0.80			0.52	0.24	0.38		2.1
Ib$_2$		0.97	0.97	0.97			0.51	0.29	0.40		2.4
		Average **0.97**	**0.81**	**0.89**			0.52	0.27	0.39		2.3
Ia$_1$	August 18	0.74	0.16	0.45	0.18	August 18 20:00	0.29	0.14	0.22	0.64	2.0
Ia$_2$		0.84	0.84	0.84			0.32	0.17	0.24		3.5
Ia$_3$		0.97	0.89	0.93			0.34	0.16	0.25		3.7
		Average 0.85	0.63	0.74			0.32	*0.15*	0.24		3.1
Ib$_1$		0.67	0.62	0.65			0.32	0.18	0.25		2.6
Ib$_2$		0.91	0.82	0.86			0.26	0.17	0.21		4.1
		Average 0.79	0.72	0.76			0.29	0.18	0.23		3.3
Ia$_1$	August 19 10:00	0.51	0.35	0.43	0.06	August 19 20:00	0.21	0.16	0.18	0.67	2.4
Ia$_2$		0.38	0.32	0.35			0.24	0.21	0.22		1.6
Ia$_3$		0.40	0.35	0.37			0.21	0.13	0.17		2.1
		Average 0.43	0.34	0.38			*0.22*	0.17	*0.19*		2.0
Ib$_1$		0.37	0.22	0.30			0.20	0.13	0.17		1.8
Ib$_2$		0.37	0.23	0.30			0.18	0.13	0.15		2.0
		Average 0.37	*0.23*	*0.30*			*0.19*	*0.13*	*0.16*		1.9

Ia_1.......	August 20 11:00......	0.31	0.18	0.24	0.08	August 20 21:00.....	0.27	0.27	0.27	0.27	0.89*
Ia_2.......		0.30	0.21	0.26			0.27	0.19	0.23		1.10
Ia_3.......		0.31	0.24	0.27			0.25	0.24	0.25		1.10
		Average 0.30	0.21	0.26			0.26	0.23	0.25		1.00
Ib_1.......		0.33	0.24	0.28			0.38	0.32	0.35		0.80
Ib_2.......		0.30	0.33	0.32			0.44	0.41	0.43		0.75
		Average *0.32*	0.29	*0.30*			0.75	0.69	0.72		0.77*
							0.52	0.47	0.50		0.91
Ia_1.......	August 21 11:00......	0.20	0.15	0.18	0.06	August 21 21:00.....	0.83	0.29	0.56	0.24	0.34
Ia_2.......		0.26	0.17	0.22			0.60	0.37	0.49		0.45
Ia_3.......		0.23	0.12	0.18			0.28	0.24	0.26		0.69
		Average *0.23*	*0.15*	*0.19*			0.57	0.33	0.44		0.43
Ib_1.......		0.39	0.17	0.28			0.78	0.43	0.61		0.46
Ib_2.......		0.31	0.17	0.24			0.59	0.42	0.51		0.47
Ib_3.......		0.67	0.62	0.64			0.27	0.27	0.27		2.30
		Average 0.46	0.32	0.39			0.54	0.37	0.46		0.87
Ia_1.......	August 22 11:00.....	0.69	0.29	0.49	0.04	August 22 21:00.....	0.70	0.60	0.65	0.66	0.75
Ia_2.......		0.34	0.21	0.27			0.73	0.73	0.73		0.37
Ia_3.......		0.24	0.15	0.19			0.73	0.63	0.68		0.30
		Average 0.42	0.22	0.32			**0.72**	**0.65**	**0.69**		0.46
Ib_1.......		0.62	0.50	0.56			0.80	0.83	0.82		0.68
Ib_2.......		0.48	0.29	0.38			0.85	0.82	0.83		0.46
Ib_3.......		0.34	0.28	0.31			0.43	0.42	0.42		0.74
		Average 0.48	0.36	0.42			**0.69**	**0.69**	**0.69**		0.61

---

* Since the experiment has been in progress a new leaf has become of sufficient size so that it was large enough for the application of the clip. For August 21 then the index 0.72 is much higher than any of the others. This will naturally increase the average. In computing the average for the index, this last number was not used; 0.77 is the average for leaves Ib_1 and Ib_2.

same series were used for the determination of wilting according to the method of BRIGGS and SHANTZ. The results are given in table II; those obtained giving the residual moisture at the time of wilting agree rather closely for the determinations made according to the two methods. In the method of BRIGGS and SHANTZ there is a greater variation than is found to be present where the hygrometric paper is used.

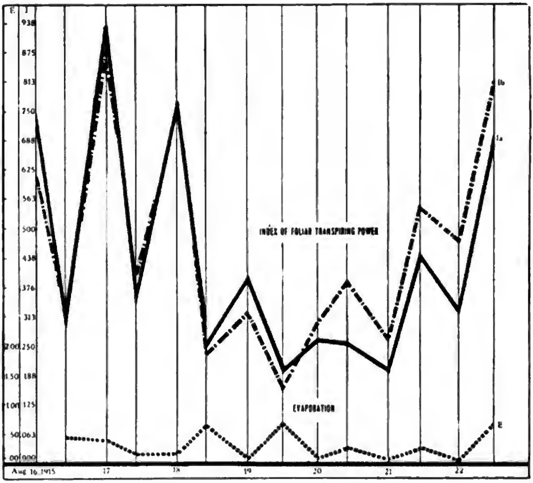


FIG. 1

TABLE II

Method	1	2	Average
Briggs and Shantz..........	10.38	7.84	9.11
Hygrometric paper..........	8.20	8.34	8.27

The breaking point occurring on August 21 is not far from the normal minimum value of the daily march of foliar transpiring power. From previous work upon the march of foliar transpiring power, there is more or less of a definite maximum (usually during the day) as well as a definite minimum (usually during the night). It seems that, in all probability, the minimum in the foliar transpiring power indicates approximately the greatest resistance to transpirational water loss. If the water content of the soil coupled with the evaporating power of the air is of such magnitude as to increase the resistance to the passage of water, so that the day maximum has a value as low or lower than the diurnal minimum (at night), the plant is then in a critical condition; at least this has been found to be true for *Helianthus*. For the entire leaf surface the transpiring power ratios at night are as follows: (1) I*a*, —0.23, 0.30, 0.34; (2) I*b*, —0.30, 0.31. On August 20 the respective values are 0.24, 0.26, 0.27 for Ia_2, and 0.28 and 0.32 for Ib_2. The average ratio for the first is 2.2 and the average ratio for the test on August 20 is 0.91. On August 21 the ratio is less; on the following day it is a little higher.

The entire situation as here brought forward centers about the amount of moisture present in the soil during the march of wilting when the index of transpiring power ratio of day to night comes to be represented by unity or less. The duration of this ratio may be an important factor in obtaining data that will give information on the relative drought resistance of plants.

Series of 1916

METHOD

The method of procedure in the experimentation for 1916 was much the same as for the previous season. The sheet iron containers were a little deeper (7 inches instead of 6). The soil mixture was lighter than before, containing 1 part of clean pure sand mixed with 3 parts of rich garden soil, and the variety the same as before (Mammoth Russian). The seeds were planted on June 24, and on July 1 the seedlings were 5 cm. high and were then transplanted. Three plants were set deeply in the soil. The cultures were then placed in the greenhouse and were watered from time to time. A Livingston standard atmometer of the cylindrical form was set up in close proximity to measure evaporation. Readings were taken of the atmometer whenever a reading was made of the transpiring power. On July 19 the plants were thoroughly watered and were lightly watered again on July 20. On July 21 the containers were sealed over with plasticine preparatory to making hourly readings of the foliar transpiring power for a period of twenty-four consecutive hours. For the measurements upon the index of foliar transpiring power the same apparatus as employed before was used. On the 18th hour of July 22 the last reading was made for the daily march of foliar transpiring power. Beginning July 24, readings were taken three times during the day: (1) at approximately 10:00 A.M., (2) at the 14th or 15th hour, and (3) at some time during the night. The times chosen really represent the three important periods during the daily march, for the first one gives this value at a time when the transpiring power is near its maximum, the second when evaporation is at its maximum, and the third when the index of transpiring power has its lowest value. The leaves were tagged as before so that the same leaves were used throughout.

The soil surface of several additional plants was coated over with plasticine to serve as a comparison or check for the plants used for the determination of foliar transpiring power. In applying the cobalt paper squares from day to day, it became easy to judge the condition of the plant. When plants presenting a physical state such as was in evidence for leaf Ia_2 on August 3, and for leaf Ib_2 on August 7, were placed in a moist chamber, they failed to recover. It was then deemed unnecessary to test further. At the time of the beginning of the experiment plant I*a* was 25 cm. high, while plant I*b* was 28 cm. high.

INDICES OF FOLIAR TRANSPIRING POWER

In using the method of standardized hygrometric paper for the determination of the indices of foliar transpiring power, two separate plants were used. The method of numbering the leaves was the same as for the 1915 series. From plant I*a* two leaves were chosen, Ia_1 having the dimensions 5×8 cm., and Ia_2, 4×6 cm.; from plants I*b* two leaves were chosen, Ib_1, 7×9 cm., and Ib_2, 3×4 cm. Whenever a new leaf became sufficiently large for the application of the clip, approximately 3×4 cm., it was included with the others. The readings were begun on the 18th hour of July 21 and continued at hourly intervals for 24 hours. Readings were taken at the same time from a standardized Livingston cylindrical form of atmometer. The results for plant I*a* are given in table III.

This series shows that the march of the foliar transpiring power is the same as has previously been pointed out (**2, 4, 28, 40**), in that the maximum transpiring power is attained at a time previous to the greatest evaporation. The highest index occurs usually at the 10th and 11th hours, while the evaporation maximum occurs usually on the 14th hour. On account of the larger number of readings it is to be expected that the graphical representation (fig. 2) will show less abruptness than has formerly been presented.

Recalling that the leaf represented by Ia_1 is older than Ia_2, it is plain that the index of foliar transpiring power is higher for the younger leaf almost entirely throughout the 24-hour period. The maximum for Ia_1 is at the 11th hour, when it is 0.93. This value is again in evidence 2 hours later. For Ia_2 the highest value is at the 10th hour, when the transpiring power value is 1.00. This same value is again reached at the 12th hour. It is evident that the younger leaf Ia_2 reaches its maximum at an earlier period than the older leaf Ia_1. This feature substantiates similar conclusions reached by BAKKE and LIVINGSTON. Another important feature in connection with the graph showing the march of foliar transpiring power is the sudden drop for both leaves. The lowest point (0.59 for Ia_1 and 0.67 for Ia_2) occurs on the 14th hour. At the 15th hour the index values are respectively 0.91 and 0.93, while the corresponding values at the 13th hour are 0.93 and 0.83. Although the drop is the feature in the afternoon readings, the recovery occurring at the 15th hour is always below that of the forenoon maximum. In the present case there is not much difference, being 0.91 for Ia_1; for the younger leaves there is a greater variation, being 0.93 at 15:00 o'clock and 1.00 for the 10:00 and 13:00 o'clock readings. At the 14th hour the average reading for the

TABLE III

DATA FOR MARCH OF INDICES OF FOLIAR TRANSPIRING POWER FOR *Helianthus* PLANT I*a* (MAXIMA IN BOLD FACED TYPE, MINIMA IN ITALICS)

LEAF NUMBER	TIME OF OBSERVATION	TIME OF COLOR CHANGE IN SECONDS		INDEX OF TRANSPIRING POWER			EVAPORATION FROM STANDARDIZED ATMOMETER, CC. PER HOUR
		Lower surface	Upper surface	Lower surface	Upper surface	Entire leaf	
	July 21						
Ia_1	18:15	31	52	0.77	0.46	0.62	
Ia_2	18:20	24	46	**1.00**	0.52	0.76	
Ia_1	19:10	42	65	0.68	0.44	0.56	0.22
Ia_2	19:15	38	55	0.75	0.52	0.64	
Ia_1	20:15	46	59	0.62	0.49	0.56	0.15
Ia_2	20:20	40	54	0.73	0.54	0.64	
Ia_1	21:10	45	72	0.64	0.40	0.52	0.16
Ia_2	21:10	40	50	0.73	0.58	0.66	
Ia_1	22:10	51	77	0.61	0.40	0.51	*0.09*
Ia_2	22:15	40	65	0.78	0.48	0.63	
Ia_1	23:10	56	74	*0.57*	0.43	*0.50*	0.15
Ia_2	23:10	45	69	0.71	0.46	0.59	
	July 22						
Ia_1	24:10	50	90	0.66	*0.37*	0.52	0.18
Ia_2	24:15	42	77	0.79	0.43	0.62	
Ia_1	1:10	48	88	0.71	0.38	0.55	0.12
Ia_2	1:15	42	74	0.81	0.46	0.64	
Ia_1	2:10	57	90	0.63	0.40	0.52	0.15
Ia_2	2:15	49	85	0.74	*0.42*	*0.58*	
Ia_1	3:10	55	85	0.65	0.42	0.54	0.15
Ia_2	3:15	50	75	0.72	0.48	0.60	
Ia_1	4:10	50	85	0.72	0.42	0.57	0.15
Ia_2	4:15	46	78	0.78	0.46	0.62	
Ia_1	5:10	50	62	0.72	0.58	0.65	0.15
Ia_2	5:15	45	57	0.80	0.63	0.72	
Ia_1	6:10	39	50	0.87	0.68	0.78	0.15
Ia_2	6:15	36	50	0.94	0.68	0.81	
Ia_1	7:10	36	42	0.81	0.69	0.75	0.15
Ia_2	1:10	36	37	0.81	0.78	0.80	
Ia_1	8:15	30	42	0.77	0.55	0.66	0.15
Ia_2	8:20	28	32	0.82	0.72	0.77	
Ia_1	9:05	24	24	0.88	0.88	0.88	0.22
Ia_2	9:05	22	22	0.95	0.95	0.95	
Ia_1	10:05	22	24	**0.95**	0.88	0.92	0.58
Ia_2	10:05	21	21	**1.00**	*1.00*	**1.00**	
Ia_1	11:00	21	20	0.91	**0.95**	0.93	....
Ia_2	11:00	20	20	0.95	0.95	0.95	
Ia_1	12:00	21	21	0.86	0.86	0.86	....
Ia_2	12:00	18	18	*1.00*	*1.00*	**1.00**	
Ia_1	13:10	16	16	0.93	0.93	0.93	1.0
Ia_2	13:10	18	18	0.83	0.83	0.83	
Ia_1	14:10	17	17	0.59	0.59	0.59	1.2
Ia_2	14:15	15	15	0.67	0.67	0.67	
Ia_1	15:10	15	16	0.93	0.88	0.91	1.2
Ia_2	15:15	15	15	0.93	0.93	0.93	
Ia_1	16:15	17	18	0.88	0.88	0.88	**1.6**
Ia_2	16:20	21	21	0.71	0.71	0.71	
Ia_1	17:00	19	19	**0.95**	**0.95**	**0.95**	1.0
Ia_2	17:00	18	20	**1.00**	0.90	0.95	
Ia_1	18:00	25	35	0.80	0.57	0.69	1.0
Ia_2	18:05	20	25	**1.00**	0.80	0.90	

older leaves (Ia_1) is 0.59 and for the younger leaves is 0.67. The differences then in the order given are 0.33 and 0.34. The respective values on the 15th hour are 0.91 and 0.93. These give recovery value differences of 0.32 and 0.26. The drop in the afternoon reading is not a new thing, either in foliar transpiring power or in transpiration. No doubt this great resistance to the

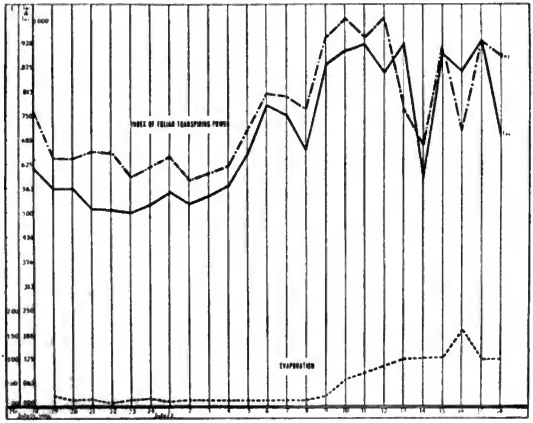


FIG. 2

passage of water is a condition of incipient drying. It may be that at this period, usually present at about the time of greatest evaporation, there is a lack of water, not only in the cells of the leaf, but also in the vessels themselves. **SHREVE** (40) has submitted evidence, at least theoretical, showing that variations in the transpiring power are due to variations in the water-holding capacity of the internal tissue. Using the **DIXON** (16, 17, 18) conception of continuous columns, as well as the results of the experiments of **RENNER** (34, 35, 36) upon transpiration, there is doubtless a greater tension present upon the water columns. If this is related to absorption and incipient drying, an additional force must be present in order to cause the water to be pulled into the cells to a greater degree than before. If this interpretation is correct, the older leaves (on account of their closer proximity to the absorption center) should show a more complete revival. This speculation would necessarily be based upon the readings of the secondary maxima. The comparative values become evident, for I*a* has a maximum of 0.93, falls to 0.59, and subsequently returns to 0.91; for Ia_2 the maximum is 1.00 and comes back from 0.97 to 0.86. This fall and subsequent rise are independent of the evaporation rate.

The march of the foliar transpiring power is more or less definite. This is especially true as it bears upon maximum and minimum values. For I*a* the maximum value occurs on the 11th hour with an index of 0.95, while the minimum value 0.50 is on the 23d hour. The ratio between maximum and minimum is 1.9. For Ia_2 the maximum value, 1.00, is in evidence on the 10th hour, while the reading 0.58 on the 2d hour of July 22 gives the minimum value. The ratio in the latter case is 1.72.

Another important feature presented by the present series is the high value on the 17th hour of July 22. In the previous experiments which have dealt with foliar transpiring power, there has been a fall in the transpiring power value after the secondary rise. It is noticed that the evaporation during the afternoon is rather intense, being 1.6. The high value of the transpiring power, therefore, is without question due to the high evaporating power of the air.

In formulating a graph (fig. 3) from the data presented in the march of foliar transpiring power, the general feature is the high foliar transpiring power before the time of greatest diurnal evaporation. For both leaves the maximum is reached at the 11th hour, when the index is 1.00. This value is retained for Ib_1 until the 12th hour, and for Ib_2 until the 13th hour. The minimum value (0.47) for Ib_1 occurs on the 22d hour, while for Ib_2 (0.44) it occurs on the 18th hour. The ratio of maximum to minimum or of day value to night value is 2.1 for Ib_1 and 2.3 for Ib_2. The sudden drop in the afternoon reading on the 14th hour is equally as striking as that

TABLE IV

DATA FOR MARCH OF INDICES OF FOLIAR TRANSPIRING POWER FOR *Helianthus* PLANT *Ib* (MAXIMA IN BOLD FACED TYPE, MINIMA IN ITALICS)

LEAF NUMBER	TIME OF OBSERVATION	TIME OF COLOR CHANGE IN SECONDS		INDEX OF TRANSPIRING POWER			EVAPORATION FROM STANDARDIZED ATMOMETER, CC. PER HOUR
		Lower surface	Upper surface	Lower surface	Upper surface	Entire leaf	
	July 21						
Ib_1	18:25	27	63	0.89	0.38	0.64	....
Ib_2	18:25	44	73	0.55	0.33	*0.44*	
Ib_1	19:25	40	67	0.72	0.43	0.58	0.22
Ib_2	19:30	44	81	0.65	0.35	0.50	
Ib_1	20:25	41	68	0.71	0.43	0.57	0.15
Ib_2	20:25	43	78	0.67	0.37	0.52	
Ib_1	21:15	44	90	0.66	*0.32*	0.49	0.16
Ib_2	21:20	39	105	0.74	*0.28*	0.51	
Ib_1	22:20	52	95	*0.60*	0.33	*0.47*	*0.09*
Ib_2	22:25	50	97	*0.62*	0.32	0.47	
Ib_1	23:15	47	85	0.68	0.38	0.53	0.15
Ib_2	23:20	43	82	0.74	0.39	0.57	
Ib_1	24:20	53	78	0.62	0.42	0.52	0.18
Ib_2	24:20	49	73	0.67	0.45	0.56	
	July 22						
Ib_1	1:20	51	78	0.67	0.44	0.56	0.12
Ib_2	1:20	47	71	0.72	0.48	0.60	
Ib_1	2:20	57	75	0.63	0.48	0.56	0.15
Ib_2	2:20	50	72	0.72	0.50	0.61	
Ib_1	3:20	46	70	0.78	0.52	0.65	0.15
Ib_2	3:20	41	70	0.88	0.52	0.70	
Ib_1	4:20	49	90	0.73	0.40	0.57	0.15
Ib_2	4:20	43	75	0.84	0.48	0.66	
Ib_1	5:20	48	82	0.75	0.44	0.60	0.15
Ib_2	5:25	40	85	0.90	0.38	0.64	
Ib_1	6:20	42	50	0.81	0.68	0.75	0.15
Ib_2	6:20	46	55	0.74	0.62	0.68	
Ib_1	7:15	31	37	0.74	0.62	0.68	0.15
Ib_2	7:15	26	42	0.89	0.55	0.72	
Ib_1	8:25	25	31	0.92	0.74	0.84	0.15
Ib_2	8:25	25	28	0.92	0.82	0.87	
Ib_1	9:10	25	30	0.84	0.70	0.77	0.22
Ib_2	9:15	21	22	1.00	0.95	0.98	
Ib_1	10:10	25	26	0.84	0.81	0.83	0.58
Ib_2	10:10	23	24	0.91	0.88	0.90	
Ib_1	11:10	19	19	**1.00**	**1.00**	**1.00**	....
Ib_2	11:10	19	19	**1.00**	**1.00**	**1.00**	
Ib_1	12:10	18	18	**1.00**	**1.00**	**1.00**	....
Ib_2	12:10	18	18	**1.00**	**1.00**	**1.00**	
Ib_1	13:15	16	16	0.93	0.93	0.93	1.0
Ib_2	13:20	15	15	**1.00**	**1.00**	**1.00**	
Ib_1	14:15	14	15	0.71	0.67	0.69	1.2
Ib_2	14:20	17	17	0.59	0.59	0.59	
Ib_1	15:20	15	15	0.93	0.93	0.93	1.2
Ib_2	15:20	16	17	0.88	0.82	0.85	
Ib_1	16:25	16	18	0.94	0.83	0.89	**1.6**
Ib_2	16:25	17	19	0.88	0.79	0.84	
Ib_1	17:10	19	18	0.95	1.00	0.98	1.0
Ib_2	17.15	20	23	0.90	0.78	0.84	
Ib_1	18:10	27	30	0.74	0.67	0.71	1.0
Ib_2	18:15	30	33	0.67	0.61	0.64	

noted for series I*a*. For Ib_1 the drop really begins on the 12th hour and falls from 1.00 to 0.69, giving a difference of 0.31; for Ib_2 the fall is from 1.00 to 0.59, giving a difference of 0.41. The recovery for Ib_1 is from 0.69 to 0.93, and for Ib_2 is from 0.59 to 0.85. The difference value is 0.24 in one case and 0.26 in the other. It was pointed out for series I*a* that the recovery of the older leaf is more marked than that of the younger leaf. This feature is again borne out in the present series, where the values for Ib_1 are in excess of those of Ib_2.

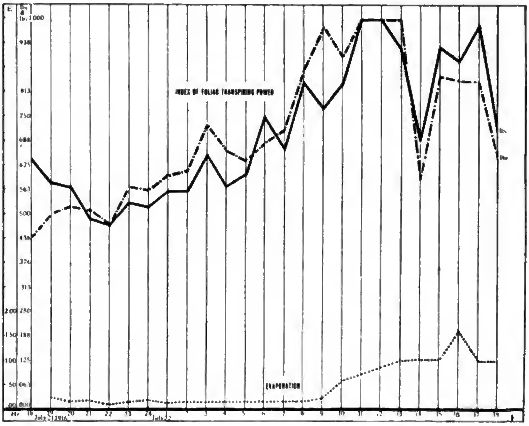


FIG. 3

For the reason that the leaves of series Ib_1 are very nearly of the same age, the same variation as set forth in the previous season will not be in evidence. The minimum values are slightly lower. As a result the ratios between maxima and minima are respectively 2.19 and 2.27. The same high foliar transpiring power is present at the 17th hour. This agrees with the former series. The data submitted in table V give the march of foliar transpiring power during the process of wilting from July 24–August 7.

TABLE V

INDICES OF FOLIAR TRANSPIRING POWER DURING PROGRESS OF WILTING OF *Helianthus* PLANT Ia

Time of observation		Index of transpiring power entire leaf		Evaporation from standardized atmometer, cc. per hour
		Ia_1	Ia_2	
July 24	9:15	0.51	0.68	1.00
	14:00	0.53	0.54	1.23
	20:00	0.28	0.39	0.73
July 25	9:10	0.49	0.29	0.24
	14:00	0.27	0.23	0.71
	21:00	0.59	0.31	0.66
July 26	9:25	0.51	0.31	0.11
	14:10	0.70	0.20	0.91
	21:15	0.49	0.21	0.62
July 27	9:25	0.43	0.20	0.02
	14:05	0.65	0.18	1.25
	22:25	0.69	0.18	0.51
July 28	9:00	0.38	0.16	0.12
	14:35	0.22	0.14	1.12
	21:00	0.36	0.19	0.66
July 29	9:20	0.33	0.18	0.13
	14:00	"	0.15	0.80
	21:00	"	0.13	0.69
July 30	9:05	"	0.21	0.28
	14:15	"	0.12	0.18
	21:00	"	0.16	0.91
July 31	10:05	"	0.34	0.26
	14:15	"	0.17	1.11
	21:05	"	0.09	0.66
August 1	10:05	"	0.17	0.24
	14:00	"	0.15	0.71
	21:05	"	0.13	0.41
August 2	10:10	"	0.14	0.24
	14:10	"	0.15	1.09
	22:45	"	0.16	0.53
August 3	10:00	"	0.14	0.34
	14:00	"	0.12	1.50
	23:00	"	0.16	0.37
August 4	10:00	"	0.17	0.22
	14:00	"	0.12	1.03
	21:00	"	0.17	1.18
August 5	10:10	"	0.17	0.33
	14:05	"	1.17	0.77
	21:00	"	0.11	0.21
August 6	9:30	"	0.14	0.11
	14:10	"	0.11	1.49
	21:00	"	0.13	1.10
August 7	10:00	"	0.13	0.49
	14:05	"	0.23	0.74

From the tabulated data of table V, and from graph (fig. 4) of series I*a*, it is noticed that there is a marked decrease in foliar transpiring power from July 24 up to the time when the plant wilts. The transpiring power of leaf Ia_1 is very irregular. There is no doubt but that the plant has attained its permanent wilting point on July 29, but because the leaves of this series are somewhat older than Ia_2, and as they are located nearer the absorptive center their action will be more or less modified by the presence of the younger leaves at the tip. For the leaf Ia_2 there is a marked decrease in the foliar transpiring power from July 24 to July 30, the foliar transpiring power being especially high on August 1. This feature is probably in response to the exceedingly high temperature at that time. The evaporation from the standardized atmometer bears out this statement. From August 1 to August 7 the index of foliar transpiring power proceeds almost in a straight line, except for small dips occurring in the majority of

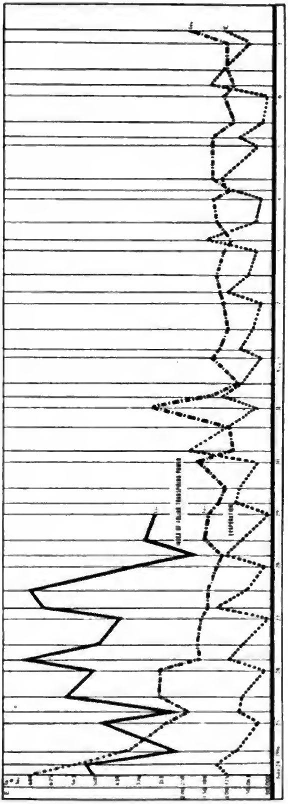


FIG. 4

cases when the evaporation was at its highest. This part of the graph conforms with the one obtained when the plants were lifted from the soil. On August 7 the index of foliar transpiring power increases from 0.13 to 0.23, or 77 per cent from the 10th hour to the 14th hour. On the previous day it dropped from 0.14 to 0.11, while on the preceding day the two indices were the same. At no other time during the march was there such a great percentage increase.

In obtaining the ratio between the day reading and the night reading for 24 consecutive hours, the day readings were usually made between the 9th and the 10th hours. For the night readings there was no need of selection as only one reading was taken. Beginning with July 24, and continuing until July 29 (time of wilting), the transpiring power indices representing the day readings for Ia_1 are 0.51, 0.49, 0.51, 0.43, 0.38, 0.33, while the corresponding night values are 0.28, 0.59, 0.49, 0.69, 0.36, 0.33. The respective ratio values are 1.82, 0.83, 1.04, 0.62, 1.05. On July 21–22 the ratio between the reading on the 9th hour and the reading on the 21st hour is 0.88:0.52, or 1.7. For the entire 24-hour period the maximum and minimum ratio is 1.9. The only normal ratio is the first. It is interesting to note that for leaf Ia_1 the minimum is normally 0.50. During the progress of wilting the maximum does not get below this point until July 27; after that it is below the usual minimum.

From July 24 to August 7 (time of wilting) the corresponding indices for Ia_2 are present; for the morning 0.68, 0.29, 0.31, 0.20, 0.16, 0.18, 0.21, 0.34, 0.17, 0.14, 0.14, 0.17, 0.17, 0.14, 0.13; for the night 0.39, 0.31, 0.21, 0.18, 0.19, 0.13, 0.16, 0.09, 0.13, 0.16, 0.16, 0.17, 0.11, 0.13. The ratio of the day (morning) readings to the night readings is respectively 1.74, 0.94, 1.11, 0.84, 1.38, 1.31, 3.78, 1.31, 0.88, 0.88, 1.00, 1.54, 1.08. For July 21–22 the ratio of maximum to minimum for Ia_2 is 1.72. For the corresponding hours the ratio is 0.95:0.66, or 1.44. On this basis, therefore, the readings of the first day are normal, in that the ratio is approximately the same as for the maximum to the minimum on July 21–22 (1.72). Also the maximum values during the march of wilting, with the exception of the first reading, are all below the minimum set during the daily march of foliar transpiring power for July 21–22.

The data presented in table VI give results that harmonize with those of table V. As was stated in connection with the march of

TABLE VI

INDEX OF FOLIAR TRANSPIRING POWER DURING PROCESS OF WILTING OF *Helianthus* PLANT 1*b*.

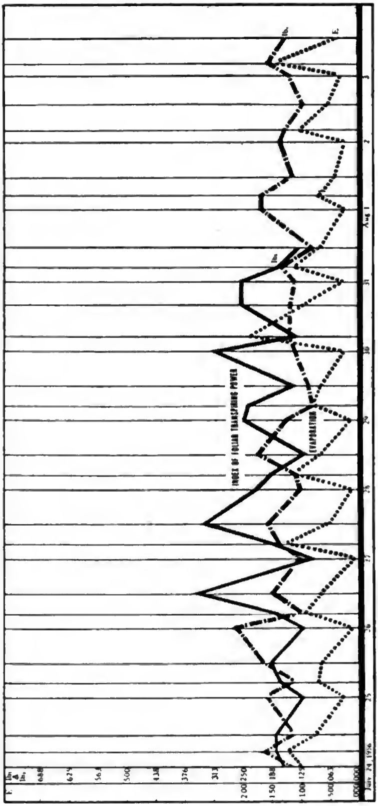
Time of observation		Index of transpiring power entire leaf		Evaporation from standardized atmometer, cc. per hour
		$1b_2$	$1b_3$	
July 24	9:20	0.17	0.15	1.00
	14:00	0.18	0.21	1.23
	20:40	0.18	0.14	0.73
July 25	9:00	0.12	0.20	0.24
	14:00	0.17	0.14	0.71
	21:10	0.19	0.21	0.66
July 26	9:35	0.12	0.28	0.11
	14:15	0.18	0.12	0.91
	21:00	0.35	0.19	0.62
July 27	9:30	0.10	0.13	0.02
	14:15	0.19	0.18	1.25
	22:00	0.34	0.20	0.51
July 28	9:25	0.22	0.13	0.12
	14:45	0.19	0.14	1.12
	21:00	0.12	0.22	0.66
July 29	9:30	0.25	0.16	0.13
	14:00	0.24	0.10	0.80
	21:00	0.14	0.11	0.69
July 30	9:10	0.31	0.14	0.28
	14:20	0.14	0.15	1.88
	21:00	0.26	0.15	0.91
July 31	10:10	0.26	0.14	0.26
	14:20	0.17	0.17	1.11
	21:15	0.13	0.10	0.60
August 1	10:10	....	0.21	0.24
	14:00	....	0.21	0.71
	21:10	....	0.14	0.41
August 2	10:15	....	0.17	0.24
	14:15	....	0.16	1.09
	22:50	....	0.12	0.53
August 3	10:10	....	0.15	0.34
	14:00	....	0.20	1.50

foliar transpiring for 24 consecutive hourly periods, the leaves selected here were closer together, and considering the relation which is present between the leaves it would be expected that the variation would not be as great.

The data given in table VI show slowly decreasing values; however, the decrease is not marked. The highest foliar transpiring power for Ib_1 is 0.35, while the lowest is 0.10. The highest point as here set forth occurs on the 21st hour on July 26, while on the following day the index at the same time is 0.34. After that there is a slight fall, although this is not true for all the readings, for on July 30 the index is 0.31. Even at the time of wilting, the index at the morning hour is 0.26. From July 29 to July 31 the maximum values are approximately the same. This is also true of the minimum values. The last reading for the Ib_1 series occurs on July 31 and gives an index of 0.13.

For leaf Ib_2 the values are strikingly similar to those of the leaf situated just below it upon the stem. The highest transpiring power index for the entire time is only 0.28, and occurs at 9:35, July 26; while the minimum value 0.10 occurs on the 14th hour of July 29 and on the 21st hour of July 31. The data of table VI, represented graphically in fig. 5, show a gradual dropping off of the day maximum values from July 26 to July 30. From July 30 to August 3, with the exception of August 1, the graph of wilting is practically a straight line. On August 3 there is a marked increase, considering that the entire period has given a low index throughout (from 0.15 to 0.20, or an increase of 33.3 per cent). Usually during the march of foliar transpiring power a drop is registered at the 14th or 15th hour. On July 27 there is an increase of the index from 0.13 to 0.18 (38.46 per cent) and on July 31 from 0.14 to 0.17 (21.43 per cent). On account of the comparatively small deviation between the maximum and minimum values throughout, the increase in the transpiring power of one-third on August 3 becomes more significant than the graph shows (fig. 5).

The ratio between the day indices and night indices is presented as before, the readings of the 9th and 21st hours being used. On July 24 the morning reading is 0.17; on the following days the average foliar indices of transpiring power for leaf Ib_1 are 0.12, 0.12, 0.10, 0.22, 0.25, 0.31, 0.26. The corresponding night values are 0.18, 0.19, 0.35, 0.34, 0.12, 0.14, 0.26, 0.13. The corresponding


E
I'h
&
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688
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2.00 250
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INDEX OF FOLIAR TRANSPIRING POWER
EVAPORATION
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FIG. 5

ratios between the day and night readings are respectively 0.95, 0.63, 0.34, 1.83, 1.79, 1.19, 2.00. The ratio between the index of foliar transpiring power for the 9th and 21st hours on July 21–22 is 1.57. The ratio between the day maximum and the night minimum at that time is 2.11.

Taking into consideration that the minimum for Ib_1 during the march of foliar transpiring power on July 21–22 is 0.49, the maximum values during the march of wilting are extremely low from the initial to the final point of wilting. On account of the drop in the maximum and the constant retentive character of the minimum, the index here is larger than recorded previously. The leaf was completely wilted on July 31.

The day values for Ib_2 taken at the same time as before are 0.15, 0.20, 0.28, 0.13, 0.16, 0.14, 0.14, 0.21, 0.17, 0.15; while the corresponding night values are 0.14, 0.21, 0.19, 0.20, 0.22, 0.11, 0.15, 0.10, 0.14, 0.12. The ratios between these two sets are, in order of their occurrence, 1.07, 0.95, 1.45, 0.65, 0.59, 1.45, 0.93, 1.40, 1.50, 1.42. The ratio between the readings for the 9th hour and the readings of the 21st hour on July 21–22 for *Helianthus* leaf Ib_2 is 0.98:0.51, or 1.92. The ratio between the maximum and the minimum is 2.23. In none of these cases can the proportion be regarded as normal. This plant from the beginning is evidently in a partially wilted state.

In comparing the march of foliar transpiring power during the process of wilting for the two series I*a* and I*b*, there would naturally be some variation. The wilting of series I*a* extends over a longer period (to August 7), while that of I*b* reaches its permanent wilting point on August 3. In both cases the older leaf wilts long before the younger leaf. However, leaf I*a* has a greater range of foliar transpiring power. Leaf Ia_1 wilts before Ia_2; likewise Ib_1 before Ib_2.

The ratio between the morning and the night readings of each day gives in the majority of cases a value that is less than the normal. For I*a* all the results are either near 1.00 or below it except for the first. As the maximum value is above that of the usual minimum the result cannot be anything but normal. With I*a* the ratio on July 31 is extremely high, probably being due to the extremely high evaporation. Why there should be such a decrease at the 21st hour is not known. The first ratio 1.74 is approximately equal to the normal. The day reading is 0.68. The ratio on August 5 is 1.54, but the 9th hour reading gives a value that is much lower than the usual minimum. With a slight decrease in the minimum, the ratio between the two becomes greater than before. From these data on the basis of the ratio between day and night foliar transpiring power values it is evident that, if the ratio is to be used during the process of wilting, it can only be applicable when the maximum is greater than the usual minimum. Throughout the series of both I*a* and I*b* the ratio does not deviate very far from unity, but in the formation of the ratio there is an evidently greater corresponding decrease in the day value as compared with the night reading. In both cases the extent of daily fluctuation for the younger leaves is very small after the first day.

The rate of evaporation throughout fluctuated considerably, but is unusually high for the climate of Chicago. There is nevertheless no close agreement between evaporation and foliar transpiring power during the march of wilting. Plants similar to the ones used in the experiment were treated like I*a* and I*b* and were placed in a moist chamber at their respective times of wilting. They behaved in a similar manner and failed to recover in the allotted time. Although the plants were watered at the same time with approximately the same amount of water, figs. 5 and 6 show indirectly that there was much difference in the soil moisture content. The plant designated as I*b* was larger than I*a*, and would be expected to wilt first. This observation is borne out in the experiment. It is also evident from an examination of the two graphs that the soil of I*b* was drier at the beginning than that of I*a*, as the indices of foliar transpiring power are much smaller.

STOMATAL DIFFUSION

The index of foliar transpiring power in its very definition is associated with that of vapor tension. The decrease in the index of foliar transpiring power such as is present at night during the daily march represents a great force. A solution may also carry with it just as great a force. LIVINGSTON (**27**), commenting upon FITTING's (**19**) work upon the osmotic pressure present in desert plants, makes the statement that with the lowering of the vapor tension 10 per cent there is represented a pressure of 100 atmospheres. In an examination of the graph in table I there is a reduction in the index from 0.92 to 0.19 during the process of wilting. This therefore represents an approximate pressure of 800 atmospheres. For plant *B* there would be an approximate pressure of 700 atmospheres. Table V and fig. 4 give leaf Ia_1 as being able to withstand a pressure of 666 atmospheres and leaf Ia_2 860 atmospheres. Leaf Ib_1, with an index 0.10, suggests a pressure as high as 900 atmospheres. At that time the margin of the leaf was sufficiently dry so that the clip could not be used without causing injury. This status becomes all the more pertinent when it is compared with the data submitted by SHULL (**41**), where the force present in air dry seed (*Xanthium*) is equivalent to 1000 atmospheres.

During the daily march of foliar transpiring power there is usually considerable variation (figs. 2, 3), even when a plant is supplied with an optimum amount of water. The sudden rise in the foliar transpiring power immediately after sunrise, as set forth by BAKKE and LIVINGSTON, gives credence to the view that the stomata open quickly at this time. In using the porometer and standardized cobalt paper squares simultaneously, TRELEASE and LIVINGSTON (**42**) find that during the daily march there is considerable agreement between the porometer readings and the readings of the foliar transpiring power by the method of standardized cobalt chloride paper. From the results obtained in their investigation they concluded that the porometer gives readings which show the extent of stomatal diffusion.

DARWIN (**12, 13**), using the horn hygroscope and the temperature method, has shown that during wilting there is a temporary opening of the stomata. DARWIN and PERTZ (**14**), using the porometer, have demonstrated that a similar condition is present during wilting. LAIDLOW and KNIGHT (**26**) in their work upon stomatal behavior during wilting, where they employ a recording porometer, have confirmed the results of DARWIN and PERTZ, in that the stomata open temporarily during wilting. For *Phaseolus* *vulgaris* the maximum diffusion occurred about 5 minutes after the leaf was severed from the stem, while in the case of the thick leaf of *Prunus Laurocerasus* nearly 20 minutes elapsed before the maximum stomatal opening was reached. KAMERLING (**23**) found that when *Rhipsalis cassytha* had lost 1 to 4 per cent of its normal water supply, the amount of transpiration per unit time increased, and later when the loss in weight had reached a certain point, varying from 6 to 10 per cent, the transpiration again diminished. KAMERLING is of the opinion that the increase in transpiration is due to the opening of the stomata. LLOYD (**31**), on the other hand, failed to find this temporary opening.

The evidences at hand support the conclusion that the stomata open for a short time during wilting. The time is short, however, and there is no evidence that the stomata ordinarily open up during the early stages of wilting and continue to be open until the plant has attained its permanent wilting point. This point is important in connection with argument presented for the break in the water columns.

In order to prove that the stomata open only during the early stages of wilting, the porometer as modified and used by KNIGHT (**24**) was resorted to. The plant was attached to the aspirator and allowed to remain until the leaves were partially wilted. Tests were made upon plants grown in the greenhouse and later transferred to the laboratory and plants which had been grown continuously in the greenhouse. The plants in the laboratory were kept for 5 days before experimentation was begun. The tests of this series were begun on November 28, 1917, and continued until December 3, 1917; readings were made at three different times of the day. This conforms with the plan adopted in making the readings of the foliar transpiring power. Evaporation was recorded by means of a standardized cylindrical form of atmometer of the Livingston type. The data are given in table VII.

In an examination of the data presented in table VII, readings were not taken until the 16th hour on November 29, 3 days after all watering had ceased. The time elapsing between two successive bubbles, as ascertained by means of a stop watch, was found to be 160 seconds. At the 11th hour it took 140 seconds, while on December 1 at 10:30 it took 246 seconds. From that time until December 3 there was not much variation either at night or during the day.

TABLE VII

POROMOTER READINGS DURING PROGRESS OF WILTING OF A *Helianthus annuus* PLANT GROWING IN LABORATORY

Time of observation	Rate of evaporation from standardized atmometer, cc. per hour	Rate of flow, time interval in seconds between successive bubbles
November 27 16:00....	....	....
28 8:00....	....	....
28 15:30....	1.45	....
29 16:00....	0.72	160
30 11:00....	1.12	140
30 14:30....	0.79	150
30 20:00....	1.34	146
December 1 10:30....	0.97	246
1 14:30....	1.11	266
1 20:00....	0.54	259
2 10:30....	1.79	276
2 14:30....	1.71	260
2 20:00....	1.41	262
3 10:30....	1.70	269

The data of the series grown continually in the greenhouse, where the evaporation was very low, are given in table VIII.

These results, which were obtained at regular intervals on 5 successive days (November 29 to December 3, 1917), do not show any marked differences. Considering the experimental error which would be present, there is not sufficient difference in any one case to indicate that stomatal movement was present. The plants used in this series were not watered for 3 days before the beginning of the experiment.

The stomatal diffusion as measured by the porometer was also determined for plants which were grown for the same period, but were not subjected to any extended period of wilting. The general average for the stomatal diffusion as represented by the time interval between successive bubbles of the air intake tube of a porometer was found to be 105 seconds. No attempt was made to ascertain whether or not the stomata were partially closed or whether there was an increased opening after a period of 2 hours, as has been shown for certain plants by Iljin (**20**). At any rate, the time interval in the case of intensely wilted *Helianthus* plants is much smaller. Even if the stomata should be partially closed, the results obtained from tables VII and VIII show that during the march of wilting, where the plant acquires its permanent wilting point, the stomatal opening does not enter in to affect the diffusion or transpirational water loss. This statement is in agreement with that of Darwin, that when the transpiration is high and the supply water insufficient the lack of water is a more important factor than stomatal changes. It would be extremely advantageous, however, to have the stomatal movement question

TABLE VIII

Porometer readings taken of a wilting *Helianthus* plant growing where evaporating power of air is low

Time of observation		Rate of evaporation from standardized atmometer, cc. per hour	Rate of flow, time interval in seconds between successive bubbles
December 11	16:00....	....	....
12	13:00....	0.35	....
	16:30....	0.23	....
13	10:30....	0.34	....
	14:30....	0.65	....
	20:00....	0.45	....
14	10:30....	0.37	357
	14:30....	0.60	360
	20:00....	0.34	352
15	10:30....	0.30	318
	14:00....	0.36	309
	20:00....	0.40	335
16	10:30....	0.43	357
	14:30....	0.43	348
	20:00....	0.49	343
17	10:30....	0.40	341
	14:30....	0.44	365
	20:00....	0.37	343
18	10:30....	0.34	308
	14:30....	0.44	389
	20:30....	0.39	360

settled. Regarding the stomatal diffusion as a minor factor during intense wilting, the problem resolves itself to the point where the resistance to the passage is considered. From the data given in this paper and in a previous publication the resistance is exceedingly great. This will give further information, therefore, upon the strength of the evaporating force and that of cohesion.

Discussion

In comparing the results obtained during the summer of 1915 with those of 1916, considerable additional evidence is set forth which substantiates the argument advanced by BAKKE that wilting occurs at a definite point and is readily determined by the use of standardized hygrometric paper. In the series of 1915 the average of 3 leaves were used in plant I*a* and 2 leaves for plant I*b*. No effort was made during the 1915 season to obtain the difference in the time of wilting for leaves of different ages. The difference, however, was probably very slight, as the evaporation was exceedingly low. At no time during the entire run was the evaporation as high as 0.7 cc. per hour, and usually it was below 0.5 cc. per hour. The temperature of the greenhouse was seldom over 28° C.

In contrast, the evaporation during the season of 1916 was high and during the time the experiments were being performed was exceedingly uniform. It may be added that during the progress of the experiment no rain fell. It would then have been preferable to have run the experiments outside, but in the climate of Chicago it is rather difficult to obtain such a continued period of clear weather. The usual feature will then be a low evaporation at night, a higher one during the forenoon, and the maximum at the 14th hour. The high evaporation rate on July 31 is not explainable. It may be well to remark, however, that on July 30 the temperature in the greenhouse was 41.2° C. and at the first hour of July 31 it was 27° C., almost the maximum of the previous year.

It is again brought out that for the 1915 and 1916 series a point is reached where the foliar transpiring power shows very little fluctuation. In the cases presented, this point can be represented graphically by a line that is almost straight. The ratio values are not far above unity in the majority of cases, and sometimes are even lower. It is noted also that the time element of this period varies greatly in the two seasons. In 1915 it is comparatively short, while for both series in 1916 it is extended over a considerable period. It has been proved by the work of SHREVE (**34**) that plants grown under different environment not only have different anatomical characters but also have a different rate of transpiration.

On the basis therefore of a possible change as a result of environment, it can safely be asserted that this is the reason for the short span in 1915 and the long one in 1916. Why or how the plant establishes such an apparent equilibrium cannot be stated. This equilibrium represents the greatest force or tension which can be applied before a plant assumes the condition of permanent wilting. A plant such as *Atriplex* will necessarily have an extended period when this equilibrium is maintained. The exact wilting will be when there is a serious rupture in the water columns.

If this interpretation is correct, the 1915 and 1916 series should exhibit a difference in the foliar transpiring power values during the so-called equilibrium stage. It would be expected that the 1915 series would have a higher minimum than the 1916 series. This is evident, for in 1915 the lowest point reached at any time is never below 0.15, while for the 1916 series it is as low as 0.09 in one case and 0.10 in the other. There would thus seem to be a direct relation between the time of the equilibrium, the lowest point in the index of foliar transpiring power, and the evaporating power of the environment. The point at which wilting occurs is definitely marked out. This point appears graphically to better advantage for the plants of 1915 than for those of 1916; but the plants of 1915 were larger and were grown in smaller containers than those of the following year. For the series of 1915 the permanent wilting occurs on August 21, while for series I*a* (1916) the wilting occurs on August 7, and for series I*b* of the same year the wilting occurs on August 4.

In this study the same conception of wilting is advanced as before. The present study is really more or less of an elaboration of the former. It is assumed here that DIXON'S (**16, 17, 18**) conception of continuous water columns is in force. When the force of evaporation becomes sufficient to cause a serious rupture of these water columns, then the plant wilts. Just to what extent a serious rupture can be regarded cannot be stated, but it must be greater than the force of cohesion which holds the water particles together.

The extent of this cohesion force has been sufficiently presented and advanced by DIXON (**16, 17, 18**), RENNER (**34, 35, 36**), URSPRUNG (**43, 44, 45, 46, 47**), and others (**21, 32**), and although the conclusions have been criticized by JOST (**22**), nevertheless they are substantiated. It is not the province of this article to enter into a critical discussion of these various papers. The approximate point of permanent wilting is readily ascertained from the beginning by taking a series of readings of the foliar transpiring power of the plant in question. Care should be taken to obtain in the series the maximum and minimum. Although there is not any hard and fast relation between the maximum and the minimum, when the moisture in a soil has been reduced to the point where the maximum is below the normal minimum, at a time of the normal maximum, then the water content of that soil has attained what the writer designates as the critical content. From this point it is simply a question of time when the columns break. This then becomes a relatively simple matter.

The readings giving the indices of foliar transpiring power taken at hourly intervals present a graph that is similar to graphs set forth previously. The maximum occurs at a time previous to the highest evaporation; the minimum generally occurs somewhere between the 18th hour and the 24th hour. There is a decided drop in the afternoon, which occurs at a time of day when evaporation is at its height or nearly so. There is a recovery that is also conspicuous. The cause for this resistance has been advanced by SHREVE (**40**) as being due to the imbibitional forces of the cell wall and of the colloids of the protoplasm. Although this feature has been noticed wherever the march of foliar transpiring power has been obtained, no one as yet has set forth any evidence as to the length of time necessary for recovery to take place. It is apparent that the recovery has been complete before the time of the beginning of the next reading, which in this case is the next hour. A record of the foliar transpiring power at hourly intervals at Chicago gives results that are similar to those obtained for plants of the same species in southern Arizona.

The series of 1916 show conclusively that the older leaves are the first to wilt. In an examination of series I*a* the older set of leaves is almost completely dry at the time of the permanent wilting of the plant. On July 29 the edges of the leaf are dry, but at the same time there is a different form of response in the younger leaves, in that the apparent recovery occasioned at the time of permanent wilting does not present itself. The same situation is true for the series I*b*, where the older leaves wilt on July 31. That the older leaves are the first to wilt has previously been determined by a number of investigations (**15, 33**). BAKKE and LIVINGSTON have presented evidence that there is considerable variation in the index of foliar transpiring power of young and old leaves. The fact that the younger leaves wilt later than the older leaves is not necessarily connected with the environment. This is true whether the evaporation is low or whether it is high. The production of the absciss-layer may at least be indirectly formed as a result. PRINGSHEIN (**33**) previously has shown that young leaves retain their freshness for a longer time than older ones. This he ascribes to a greater osmotic pressure. During the march of wilting it is also noticed that the foliar transpiring power index of the older leaves is always higher, at least than that of the leaves of the tip. The older leaves then give a higher foliar transpiring power throughout.

There is also in evidence during the march of wilting not only a low index of foliar transpiring power, but also a gradual increase of the force in opposition to the passage of water. When for a short time there is an evident break or a serious rupture, there is a decrease in the resistance, but an equilibrium with the atmosphere is soon reached. The assumption that there is a temporary opening of the stomata may be made at this point. Employing the porometer upon *Helianthus* plants placed in an environment of high evaporating power and one of low evaporating power, the author failed to find that the stomata are concerned.

Summary

1. The transpiring power of plants as determined by standardized hygrometric paper gives an accurate knowledge of the internal water relations of a plant. The exact wilting point as determined by this method occurs when there is a serious rupture in the water columns.

2. During the daily march of foliar transpiring power obtained by making consecutive hourly readings for 24 hours, the maximum is attained at a time previous to the greatest evaporation. During the time of approximate maximum evaporation there is a marked fall in the foliar transpiring power index, followed shortly by a rise. The ratio between the maximum and the minimum is more or less definite, but not sufficiently so for the formation of any law. When the ratio is reduced to the point where it is in the neighborhood of unity, the plant is in a state of intense incipient drying. When the maximum value does not exceed the usual minimum, the plant is in a soil environment which is critical from the point of water supply, or almost at its wilting coefficient. It is then merely a question of time before the plant wilts.

3. Evaporation plays an important part in the experiment upon transpiration. A high evaporation gives an increased transpiring power value, but during the process of wilting the index of foliar transpiring power comes to be independent of evaporation.

4. During the process of the march of wilting an equilibrium point is reached where the indices of foliar transpiring power do not show much variation. It is suggested that the duration of the equilibrium gives a measure of the comparative drought resistance of different plants. *Helianthus* grown in 1915 during a rainy season is different from *Helianthus* grown during 1916, when the season was unusually dry. The equilibrium period of 1915 was much shorter than for 1916.

5. There is a decided difference in the time at which permanent wilting occurs in old and young leaves. The older leaves will wilt long before the younger ones. The time interval varies according to age.

6. Stomatal movements or changes are not important factors when the plant is in an intense state of wilting.

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NOTES ON AMERICAN WILLOWS

I. THE SPECIES RELATED TO SALIX ARCTICA PALL.

CAMILLO SCHNEIDER

The more I advance in the study of American willows the more I realize that every species and form needs thorough investigation, and that even the most common and apparently best known species are far from being well understood in their variation and relationship to other forms. It will take two years more before I shall be sufficiently acquainted with all the American species hitherto described and preserved in the leading herbaria of this country to undertake their final arrangement in a monograph. At the advice of Professor SARGENT, therefore, I shall prepare, in the course of my studies, a series[1] of papers dealing with those species and forms which I have had an opportunity to investigate as thoroughly as can be done with herbarium material only. In November 1917 I commenced an investigation of the willows treated by RYDBERG in his paper entitled "Caespitose willows of Arctic America and the Rocky Mountains" (Bull. N.Y. Bot. Gard. **1**:257. 1899). I received from the New York Botanical Garden and from the Herbarium of the Geological Survey of Canada at Ottawa the material that RYDBERG had before him. Besides this I had at my disposal the splendid collections of the Gray Herbarium, the Missouri Botanical Garden, and of course of the Arnold Arboretum. Furthermore, I was able to see the Labrador material of the Bebb Herbarium, now in the Herbarium of the Field Museum at Chicago, and also very interesting collections made in Labrador, Greenland, and Alaska from the Herbarium of Cornell University. I take this opportunity to offer my best thanks to the gentlemen in charge of all these herbaria. Unfortunately I have not been able to look over the rich collections of the U.S. National Herbarium at Washington.

It would have been of the greatest advantage if I could have seen the material collected by LUNDSTRÖM and used in his "Kritische

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[1] For my first paper see BOT. GAZ. **65**:1–41. 1918.

Bemerkungen über die Weiden Nowaja Semljas und ihren genetischen Zusammenhang" (Act. Reg. Soc. Sci. Upsala III. 1877), for without comparing a good series of specimens of *S. arctica* and *S. glauca* from Northern Asia and Europe it is difficult to get a correct understanding of those forms from North America; but at present it is impossible for me to consult any European herbarium.

In this article I shall try to present a critical account of the species related to *S. arctica* Pall.; in a following paper I intend to discuss *S. glauca* L. and the species related to it; while in a third paper a key will be given containing the species treated in the first two papers and also those of sections RETICULATAE and HERBACEAE (RETUSAE), together with a few other species the systematic position of which is not yet fully understood, but which are best placed near one or the other of the groups in question. In this key it is intended to indicate briefly the main characters of the species, because full descriptions cannot be given here except of the new species and varieties I wish to propose.

The history of most of the species must be explained, I am sorry to say, at considerable length, since otherwise it would be impossible to account for the fact that so many well marked types have been interpreted so differently by various authors. I commence with *S. arctica* Pall., which is the nucleus of the group of forms I shall try to elucidate.

1. S. ARCTICA Pall., Fl. Ross. 1²:86. 1788.—PALLAS described this species from the "plaga arctica muscosa nuda secundum Sinum Obensem et versus glacialem Oceanum" in such an unmistakable manner that it could never have been misunderstood had not ROBERT BROWN, in 1819, proposed a new *S. arctica*, ignoring altogether the older name of PALLAS. In ROSS, Voy. Expl. Baffin's Bay (appendix, p. 148, and ed. 2, **2**:194, both in 1819), BROWN mentioned only the name, and a description of his *arctica* was first given by RICHARDSON in FRANKLIN, Narr. Jour. Polar Sea, Bot. App. 752 (reprint, p. 24). 1823. In the same year BROWN published his own description in Chloris Melvilliana, which was issued separately, while Capt. PARRY'S Voyage, of which the Chloris is only a part (App. Suppl. pp. 259–305), did not appear until 1824; but in 1823 there also appeared a second edition of FRANKLIN'S book and

RICHARDSON's Appendix. Later, in the synonymy of *S. anglorum* Cham., I shall give the full and exact quotations of *S. arctica* Br.

The earlier *S. arctica* Pall. has also been overlooked by KOCH (1828), who mentioned only BROWN's species. The first author who recognized the two discrepant *arctica* seems to have been MEYER (De Plant. Labrad. 32. 1830), where in a note to *S. arctica* Br. he says, "Quid est *Salix arctica* Pallas (florae rossicae II. pag. 170 editionis minoris)? Nullibi eam vel ut peculiarem speciem, vel ut synonymon apud botanicos memoratam inveni." In 1831 CHAMISSO (Linnaea **6**:541) proposed the name *S. anglorum* for *S. arctica* Br., non Pallas; see under *S. anglorum*.

In 1832 TRAUTVETTER, in his valuable study "De Salicibus frigidis Kochii," described the 3 following species: *S. crassijulis* Trev., *S. diplodictya* Trvt., and *S. torulosa* Led. Of these in 1833 (in LEDEBOUR, Fl. Alt. **4**:283) he referred *S. crassijulis* and *S. torulosa* as synonyms of *S. arctica* Pall., which had not been mentioned by him in 1832. In this year he described and figured only a *S. arctica* Br., which in 1833, however, he says is nothing but a synonym of *S. glauca* L. In MIDDENDORFF, Reise Sib. **1**^{2}:27 (Florul. Taimyr.), TRAUTVETTER again changed his opinion, saying, "*Sal. arcticam* Pall. et *Sal. arcticam* R. Br. unam eandemque speciem sistere opinor. Planta, quam in dissertatione de Salicibus frigidis N. 7. tab. VI. sub nomine *Sal. arcticae* R. Br. proposui, ad *Sal. glaucam* L. referenda est nec sistit veram *Sal. arcticam* R. Br., uti e descriptione cel. R. Brownii in Fl. Melv. l.c. elucet." See also under *S. anglorum*.

In 1849–51 LEDEBOUR (Fl. Ross. **3**:619) included under *S. arctica* Pall. BROWN's species as well as TRAUTVETTER's 3 species of 1832, and also added to *S. arctica* such forms as var. *minor* (*S. phlebophylla* And.) and var. *leiocarpa* (*S. rotundifolia* Trev.). LEDEBOUR seems to have been the first author who mentions *S. anglorum* Cham. in the synonymy.

In a strange way the forms related to *S. arctica* have been treated by ANDERSSON (DC. Prodr. **16**^{2}:285. 1868), who, in 1858, in his previous work on North American willows, only mentioned *S. arctica* Br. as a "species difficile sane definienda, quasi inter *S. myrsinitidem* et *glaucam* prorsus media et formas plures ambiguas amplectens." To those "formas ambiguas" belong the 3 varieties (*subphylicifolia*, *subreticulata*, and *subpolaris*) proposed by ANDERSSON in 1858, which I have not yet been able to interpret correctly owing to lack of the type material.

In the Prodromus, ANDERSSON created a *S. Pallasii* with the var. *crassijulis* (Trev.) and var. *diplodictya* (Trvt.), and mentioned, strange to say, the type of PALLAS under the last variety, while he is using the name *S. arctica* Pall. to cover a multitude of forms including his var. *nervosa*, *Brownei*, *groenlandica*, *petraea*, and *taimyrensis*. He excluded from his *S. arctica*, therefore, the forms of the true *S. arctica* Pall., and combined under this name a series of very different things like *S. altaica* Ldstr. (recte *S. torulosa* Led.), *S. anglorum* Cham., *S. groenlandica* Ldstr., *S. petrophila* Rydbg., *S. taimyrensis* Trvt., and others.

The first who attempted to clear up the *Pallasii-arctica* mixture of ANDERSSON was LUNDSTRÖM in 1877, in his interesting study previously mentioned. He confined *S. arctica* Pall. to its typical forms, and distinguished besides *S. Brownei* (And.) Ldstr., for which *S. anglorum* Cham. is the oldest name, *S. groenlandica* (And.) Ldstr., and *S. altaica* Ldstr., in which case he overlooked the priority of *S. torulosa* Led., a species founded on the same type. LUNDSTRÖM did not use CHAMISSO'S name because, following ANDERSSON, he referred *S. anglorum* to *S. phlebophylla;* see under *S. anglorum*. Another attempt to interpret properly *S. arctica* Pall. and *S. arctica* R. Br. was made by BEBB (BOT. GAZ. **14**:115. 1889), who, however, did not know LUNDSTRÖM'S work. Consequently he proposed another *S. Brownii* which, sensu stricto, corresponds with *S. anglorum*, a name likewise overlooked by BEBB, who refers some different forms to his *Brownii*. In 1899 BALL (Trans. Acad. Sci. St. Louis **9**:89) mentioned that "the methods by which Professor ANDERSSON succeeded in greatly augmenting the then existing confusion in regard to *S. arctica* R. Br. and *S. arctica* Pall. have been exposed by Mr. BEBB," and stated that BEBB had ignored the existence of LUNDSTRÖM'S earlier homonym; but BALL, in his turn, overlooked the name given by CHAMISSO many years before. It was RYDBERG who, in 1899, reinstated the name *S. anglorum* as the oldest correct name for *S. arctica* Br., non Pall.

I have seen but one leaf of the type specimen of PALLAS. It does not possess stomata in the epidermis of the upper surface, a character upon which I am inclined to lay considerable stress. It is true that by A. and E.-C. CAMUS (Class. Saules Europe **2**:55. 1905) *S. arctica* is said to possess "stomates ... assez nombreux" in the upper leaf epidermis, but judging by their synonymy these authors include under *S. arctica* so many widely different forms that they probably did not examine a true *arctica* at all. So far as I can see, this species is represented in the New World only in Alaska, the Yukon Territory, and the adjacent part of the northwest corner of British Columbia, and in the apparently well marked var. ***subcordata*** in southern British Columbia. I am not yet quite sure how far the range of *S. arctica* extends toward the east, but it seems not to cross 130° W. longitude except in the var. ***subcordata***, of which the geographical distribution is not yet fully known. The specimen collected by BELL on Nottingham Island, Hudson Strait (no. 24623 O.[2] olim 18825), which is cited by RYDBERG under *S. arctica* Pall., belongs certainly to *S. anglorum*.

There seems to be no great difficulty in distinguishing typical forms of *S. arctica* from those of *S. anglorum* if one has well developed specimens. Very often, however, it is necessary to deal with mere fragments, and in this case the best character seems to be furnished by the presence or absence of stomata in the upper leaf surface. While they are entirely lacking in what I take for typical *S. arctica*, they are more or less numerous in all the specimens I have seen of *S. anglorum*. Generally, *S. arctica* is a much more robust plant with larger leaves and catkins and thicker branchlets, but when we compare the shape and pubescence of the leaves and the different characters of the flowers and fruits it is rather difficult to express in words those signs that the eye can more or less easily perceive. The best description of the American form of *S. arctica* is given by COVILLE in his excellent study of the "Willows of Alaska" (1901), to which is added a good plate. I shall say something more about the differences between *S. arctica* and *S. anglorum* under the latter species; otherwise I refer to the keys that will be given in my third paper.

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[2] In citing herbarium specimens I use the same abbreviations as in my first paper; see BOT. GAZ. **65**:9. 1918. There are to be added the following: C., Herb. Field Columbian Museum; Cor., Herb. Cornell University; O., Herb. Geol. Surv. Canada.

Regarding the variability of *S. arctica*, COVILLE said: "The large number of specimens examined tends to confirm the idea that the extreme variation in the leaves is chiefly an individual characteristic and does not mark recognizable incipient species. The nearest approach I have found to a subspecific differentiation is in some of the specimens from the Pribilof and St. Matthew Islands in Bering Sea, and the Shumagin Islands. In these specimens the leaves are orbicular, or nearly so, and only about 2–3 cm. in diameter, while the catkins are shorter than usual, about 1.5–3.5 cm. in length." These forms represent ANDERSSON's *S. Pallasii* α, *crassijulis* 3 *obcordata* (1868) (*S. Pallasii* var. *obcordata* Turner; *S. arctica obcordata* Rydb.), who also distinguished f. *grandifolia* and f. *oblongata* of his var. *crassijulis*. The last two forms are, I believe, without any taxonomic value, while f. *obcordata* well deserves to be mentioned as a form or even as a variety. It differs chiefly in the characters mentioned by COVILLE. In addition to the localities cited by this author, I saw specimens from the Yacutat Bay, Glacier Bay (Muir Glacier), and Unalaska which should be referred to var. *obcordata* (And.) Rydbg. The following extract from an account given by TURNER (Contrib. Nat. Hist. Alaska 75. 1886) seems to me worth quoting.

> *S. Pallasii* Anders. var. *obcordata* Anders. This species of willow attains the largest size of any among the Aleutian Islands. The growth is exceedingly crooked, rarely straight for more than a foot, attaining a diameter of 2 to 3 inches, but often decayed within. In all the valleys and wider ravines this species is found in abundance. The roots form an intricate mass, often much exposed, and with the crooked branches and trunks form an impenetrable thicket of considerable area. . . . . VEMAMINOF [a Russian traveler] states that in former years this willow grew to such a size in one of the ravines opening on the west side of Captain's Harbor at Unalaska Island that the Russians and Aleuts procured sufficient of these trunks to be used advantageously in making bidaras (open skin boats). . . . . I visited the locality to find traces of such former growth and found the willows to be of but little better size than in other places near by.

There is another form which has very glabrescent capsules and may be identical with *S. arctica* var. *glabrata* Trautvetter (Act. Hort.

Petrop. **5**:107. 1877), of which he remarks: "Solum modo ovariis et bracteis parce puberulis a var. ***typica*** recedit. Forsan *S.* ***arcticae*** proles hybrida." Without having seen TRAUTVETTER's type, which had been collected by CZEKANOWSKI and MUELLER "inter fl. Olenek et fl. Lena inferiorem, ad fl. Tyria in tundra." I am not sure whether the following plants really represent TRAUTVETTER's variety: Unalaska, Kiuliuk, September 30, 1871, *M. W. Harrington* (fr.; G.), Dutch Harbor, July 17, 1899, *B. E. Fernow* (f., fr.; Cor.), Kodiak Island, July 2–4, 1899, *B. E. Fernow* (f., m.; Cor.), and Yakutat Bay, Disenchantment Bay, August 13, 1892, *F. Funston* (no. 117 partim, fr.; Cor., M., N.). LEDEBOUR (Fl. Ross. **3**:619. 1849–51) has described a variety with entirely glabrous fruits under the name var. ***lejocarpa***, the type having been collected by ERMAN in Kamchatka in "ignivomo Schiwelutsch" (Shivelutch). This specimen, which I have not yet been able to compare, was mentioned by CHAMISSO (Linnaea **6**:541. 1840) as a form of *S.* ***arctica*** Pall., while ANDERSSON (1868) referred it to his *S.* ***Pallasii*** var. ***diplodictya***. The true *S.* ***diplodictya*** Trautv. came from the "insula St. Laurent," and its main difference from typical *S.* ***arctica*** is, according to the author's description and figure, the "folia . . . . subtus pallidiora nec glauca nec glaucescentia, utrinque lucida." I have seen no specimen with such leaves, but COVILLE states that "occasionally specimens are found which lack the glaucousness of the lower leaf surface, a character on which TRAUTVETTER based chiefly his separation of ***diplodictya***." RYDBERG, who kept ***diplodictya*** as a species, interpreted it in a very different way, and referred to it certain forms of which I shall speak under *S.* ***ovalifolia***.

The var. ***subcordata*** previously mentioned from southern British Columbia is a form that needs further investigation. It has been described by ANDERSSON in Öfvers. K. Vet.-Acad. Förh. **15**:128 (Bidr. Känned. Nordam. Pilart.). 1858; in Proc. Amer. Acad. **4**:69 (Sal. Bor.-Am. 24). 1858; in Walp., Ann. Bot. **5**:754. 1858, from specimens collected by DRUMMOND in the "Rocky Mountains." In 1890 BEBB (BOT. GAZ. **15**:55) dealt with this rather obscure plant and stated that "the specimens from which the description of this supposed new species was drawn are all attached to a single sheet in the Kew herbarium; they belong to three distinct and well known species." **Bebb** had received, through **Baker**, nothing but a drawing and copies of the labels and "a few fragments, a capsule or two, to show minute characters." Through the kindness of Sir **David Prain** the Arnold Arboretum has received (together with a series of photographs of other *Salix* types of the Hookerian herbarium) an excellent photograph of the type sheet of *S. subcordata* and also fragments of leaves and flowers. According to this material the fact stands as follows. In the upper left corner there are "two large specimens of *S. arctica* Pall." which **Bebb** believed had been labeled "almost certainly by some mistake" as "from the Rocky Mts. coll. *Drummond*" because, as **Bebb** had explained before, "nothing approximating in character to *S. subcordata* And. has been found." There are before me, however, the excellent specimens mentioned later from the Chilliwack Valley, which, in my opinion, are identical with **Drummond**'s plant. Where this collector obtained his material I cannot ascertain, and so far as I know, he did not collect in this part of British Columbia. Beneath these two "*arctica*" specimens there are 3 (not 2, as **Bebb** stated) pieces, of which the one in the left corner is sterile, while the middle one bears female and the right one male flowers. Of both of them the Arboretum received fragments which show that they represent the same species as the older branchlets above them. **Bebb** refers those flowering branchlets to "*S. cordifolia* Hook.," and he is right in so far as **Hooker** included in his *cordifolia* those Rocky Mountain forms. But **Andersson** separated in 1858 just those western forms as *S. subcordata* from the eastern ones, which he then named *S. alpestris americana* (*S. cordifolia* Hook., pro parte).

The most critical part of the type sheet is the two sterile right hand branchlets which **Bebb** stated to be "two stunted specimens of *S. adenophylla*, leaves only, habitat not given." To those branchlets refers Dr. **Barratt**'s label: "no. 92, *S. cordifolia β serrulata*." Of those pieces the Arnold Arboretum did not receive fragments, but, so far as I can judge by the photograph and by the corresponding number in Herb. N., they do not at all belong to *S. adenophylla* sensu **Bebb** (*S. syrticola* Fern.), but seem to represent a form of *S. Barclayi*, which grows together with *arctica subcordata*, at least in the Chilliwack Valley. This fact explains the confusion of the two species, and there is to me no great "mystery how they came to be placed together on the same Kew sheet." It is, however, "more inexplicable how so critical a salicologist as ANDERSSON should have been misled into combining the characters of the two in his *S. subcordata*." I have also seen the "corresponding numbers of the HOOKER, BARRATT, and TORREY distribution in the Torrey Herbarium" mentioned by BEBB. There are 3 sheets before me. One contains a large leaf and 2 sterile young branchlets, and all 3 pieces belong to var. *subcordata*. This sheet bears the following 2 labels: "No. 90. Herb. H.B. [&T., crossed out; instead of it is written beneath "fig."] *S. obovata* var. *glabra*," and "88 Barratt, Rocky Mts. Ament leafy at the base about 4 leaves—Smooth and paler beneath." Underneath the big leaf BEBB, in 1887, has written "*S. crassijulis* Trev.?, *S. subcordata* And. in part." The second sheet contains two flowering branchlets and bears the label "No. 89 Herb. H.B. & T. Rocky Mts." as well as the statement in BEBB's handwriting "*S. subcordata* And. in part." These flowering branchlets are identical with those in Herb. Kew. The third sheet bears the *Barclayi* form previously mentioned.

ANDERSSON apparently had no clear idea of his *S. subcordata;* in 1858 he stated, "Quoad habitum quasi hybrida a *S. cordata* (cujus folia habet sed breviora) et *S. glauca* (amenta!)." In 1868 he referred to it some more specimens collected by BOURGEAU and DE LA PYLAIE, which I have not yet seen. The material before me looks very much like other robust specimens of *S. arctica*, but the leaves possess some stomata in the upper surface, at least along the main nerves. I think, therefore, that it is best to keep these forms as a variety of *S. arctica*, and I use ANDERSSON's name.[3]

S. ARCTICA var. **subcordata** (And.) nov. var. seems to differ from typical *arctica* chiefly by the following characters: foliis maximis obovato-ellipticis ad 8:6 cm. vel obovali-oblongis ad 7:2.5 cm. vel ellipticis ovali-ellipticisve ad 8.5:5 cm. magnis superne stomatiferis; amentis (saltem fructiferis) permagna ad 11 cm. longis et 1.5 cm. crassis.

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[3] RYDBERG (Fl. Rocky Mts. 167. 1917) uses the name in a different sense. I am not yet quite sure what form is meant by him.

As already stated, the exact locality where DRUMMOND collected the type is unknown to me. The other material came from British Columbia: Chilliwack Valley, between latitude 49°–49° 10′ and longitude 121° 25′–122°, 1650 m., August 29. 1901, *J. M. Macoun* (no. 26909 O., fr.; G., N.); Selese Mt., 1290 m., July 25, 1906, *W. Spreadborough* (no. 79556 O., fr.; Cor., N.; 79557 O., m.; Cor., N.; 79558 O., f., fr.; Cor.; 79559 O., m., fr.; Cor.); Skeena River, Hazelton Mountains, July 13, 1917, *J. M. Macoun* (no. 95405 O., f.).

There is also a forma incerta foliis oblongo-ellipticis utrinque acuminatis, collected by *G. E. Cooley*, in Juneau, Alaska, above Silver Bow Basin, August 6, 1891 (m.; G., N.), which has been referred by RYDBERG to *S. anglorum*. In my opinion it has nothing to do with that species, but may represent a special form of *S. arctica*, under which species it is cited by COVILLE.

2. S. ANGLORUM Chamisso in Linnaea **6**:541. 1831, exclud. specim. citat.—*S. arctica* R. Brown in Ross, Voy. Expl. Baffin's Bay, app. p. 143. 1819. and ed. 2.**2**:194. 1819, nomen nudum, non Pallas; Chloris Melv. 24. 1823; Capt. Parry's Voy. App. Suppl. p. 282. 1824; Richardson in Franklin, Narr. Jour. Polar Sea 752 (reprint 24). 1823; ed. 2.765 (reprint 37). 1823.—*S. arctica* β *Brownei* Andersson in DC. Prodr. **16**²:286. 1868, pro parte.—*S. Brownei* Lundström in Nova Act. Reg. Soc. Sci. Upsala III. 1877. 37, pro parte max.—*S. Brownii* Bebb in BOT. GAZ. **14**:115. 1889, pro parte max.

As already stated under *S. arctica* Pall., the existence of this previous name had apparently been overlooked by BROWN in establishing his new *arctica*, of which RICHARDSON was the first to give a description. It may be that this diagnosis was prepared by BROWN, because RICHARDSON in his preface expressly acknowledges the great assistance BROWN gave him, but the first edition of RICHARDSON'S Botanical Appendix appeared shortly before the Chloris Melvilliana, in which BROWN published an excellent description of his species. When in 1831 CHAMISSO changed BROWN'S name to *S. anglorum* after having given a good account of *S. arctica* Pall., non Br., he said nothing but the following:

> *Salix anglorum* N.—*S. arctica* R. Brown ex Ed. Nees 1. p. 406. supl. to the append. of Cap. Parry's Voy. p. 282. E. Meyer Lab. p. 32 (non Pallas).—Insula et sinus Sti. Laurentii.—Ex insula Chamissonis, capsulis maturis vetustate calvescentibus.

These specimens, however, do not belong to *S. anglorum*, but what in 1839 HOOKER (Fl. Bor.-Am. **2**:153) referred to *S. retusa*. HOOKER, therefore, quotes *S. anglorum* in his synonymy of this species, for which ANDERSSON (1858) proposed the name *S.* (*retusa**) *phlebophylla*, and made it a species (*S. phlebophylla*) in the Prodromus (1868). Here he also quotes *S. anglorum* in the synonymy, having in 1858 ignored entirely CHAMISSO's name, which has been used by some later authors for *phlebophylla* instead of *anglorum*. RYDBERG (1899) was the first to state that CHAMISSO's name "must be regarded as equivalent" to *S. arctica* Br.

What, however, is the typical *S. arctica* Brown? It was first collected by Ross during his exploration of the "Baffin Bay, Lat. 70° 30′ to 76° 12′ on the east side, or at Possession Bay, Lat. 73°, on the west side." RICHARDSON probably based his description chiefly on his own plants collected on "barren grounds from Point Lake to Arctic Sea" (or, as the explanation in ed. 2 runs, on "barren grounds from Lat. 64° to the Arctic Sea, in Lat. 60°"); while BROWN, besides the plants of ROSS, mentioned those of PARRY's Expedition from Melville Island, Winter Harbor. I have not yet seen a type specimen, but RICHARDSON's and BROWN's descriptions are sufficient to furnish us with the following characters:

Frutex depressus. Rami, decumbentes, floriferi omnes et sterilium nonnulli adscendentes, adulti glabri. Folia elliptico-obovata vel obovata, integerrima, novella pilis sericeis vestita, adulta utrinque glabra, venis subtus parum eminentibus, venulis anastomosantibus. Amenta utriusque sexus ramos brevissimos foliatos terminantia. Squamae orbiculato-obovatae, saepe retusae, fusco-nigricantes pilis sericeis vestitae. Mascula 8–10 lin. longa, densa. Stamina 2, filamentis distinctis, antheris purpureis. Glandulae duae. Ovaria sessilia vel brevissime pedicellata, dense griseotomentosa. Stylus longitudine varians, nunc stigma aequans, nunc fere dimidio brevior. Glandula unica.

Judging by these characters, there seems no doubt what form must be taken for the true *S. arctica* Br., that is, *S. anglorum* Cham. According to TRAUTVETTER (see under *S. arctica* Pall.) there have been distributed by HOOKER specimens under the name of *S. arctica* Br. which do not belong to this species, and TRAUTVETTER (1847) says that his *arctica* of 1832 (t. VI.) is not identical with BROWN's plant. However, so far as I can judge by TRAUTVETTER's diagnosis and figure, I believe that he had the true *S. anglorum* before him. Of course, only an inspection of his type can make a final decision regarding its identity possible. Of ANDERSSON's treatment of *S. arctica* Br. I have already spoken. LUNDSTRÖM, who apparently misinterpreted the name *anglorum*, chose ANDERSSON's (varietal) name *Brownei* for what he believed to be *S. arctica* Br. I strongly suspect that *S. Brownei* Ldstr. only partly belongs to *S. anglorum*, and an investigation of LUNDSTRÖM's specimens from Nowaja Semlja is needed to decide what he really understood by his *S. Brownei*. It seems to me most unlikely that the true *S. anglorum* should at all occur on Nowaja Semlja or in Arctic Asia or Europe; and the description given by LUNDSTRÖM, in my opinion, does not fit BROWN's species. There may be in Arctic Asia and Europe similar forms which, however, in reality belong to *S. arctica* Pall.

BEBB, as already stated, unfortunately did not know LUNDSTRÖM's work when proposing a new *S. Brownii* which comprised *S. arctica* And. (1868) "excl. var. *nervosa*." He created a new mixture of forms, including *S. groenlandica*, *S. petrophila*, *S. taimyrensis*, and others. In April 1899 RYDBERG said: "There is scarcely a species that has been so misunderstood as this [*S. arctica* Br.]. Even Mr. BEBB, who cleared up somewhat the discrepancy between *S. arctica* Pall. and *S. arctica* Br., had a very vague idea about the latter." RYDBERG himself did not interpret correctly BROWN's species. He quotes as type "Franklin Expedition, Dr. *Richardson*," and cites a specimen of the "Herb. Hooker, Barratt, and Torrey, no. 93," which I have before me and which bears the label

"*S. arctica*, Fort Franklin, Mackenzie River." It contains male and female branchlets with young flowers and very young, narrowly lanceolate, rather acute leaves. So far as I can judge by the thinly pubescent and distinctly pediceled ovaries, by the oblong bracts, and by the absence of a dorsal gland in the male flowers, the specimen does not belong to *S. anglorum*, but may probably be referable to *S. groenlandica* Ldstr. Furthermore, RYDBERG states that his *S. anglorum* "is characterized by . . . . the exceedingly large catkins, which are rather loosely flowered below, and the large conic capsule, which is only moderately hairy." If we compare this statement and the specimens cited by RYDBERG, his misinterpretation of BROWN'S species is evident. RYDBERG refers to his *S. anglorum* mostly specimens that in reality belong to *S. groenlandica*, about which species he certainly had a very wrong idea.

Almost simultaneously with RYDBERG (May 1899), BALL published a statement regarding *S. arctica* and BEBB'S treatment of this species. He knew LUNDSTRÖM'S study, but overlooked *S. anglorum* Cham.; he said, however, "I shall not rename the plant now, for I believe the name which has been in use for 80 years (*S. arctica* R. Br.) can yet do duty until both the numerous variations and the synonymy have been given careful study." In BRITTON and BROWN'S Ill. Fl. (ed. 2. 1:605, *fig. 1489*. 1913) the name *S. anglorum* is applied to forms from "Labrador to Alaska, and in the Rocky Mountains to Colorado" in a way I do not understand.

Judging by the ample material before me, *S. anglorum* seems more variable than *S. arctica*. The habitat of the northeast American plant ranges from Northwest Greenland (about Disco Island) and Labrador (where it apparently does not occur south of the 55th parallel) through northern Ungava along the Hudson Strait and the northern shores of the Hudson Bay to the Franklin Bay, reaching, as it seems, its most western point at Cape Bathurst and not ranging beyond 130° W. longitude. There are some forms collected on Herschel Island (coast of Yukon Territory) which might be taken for *S. anglorum*, but on account of the absence of stomata in the upper surface of the leaves I refer them to *S. arctica*. Between 130° and 140° W. longitude there may be the meeting ground for the 2 species, and we need much more and well collected material from there to get a correct conception of the relationship of those arctic forms. I am not fully convinced that the presence of stomata in the leaf surface of *S. anglorum* and their absence in *S. arctica typica* can be regarded as a decisive character in distinguishing certain similar forms, but I think this specific character is of great taxonomic value at least in several species. A. and E.-C. CAMUS lay much stress upon this character in establishing their systematic arrangement according to anatomical features, and an excellent observer like the well known dendrologist E. KOEHNE was always inclined to pay much attention to those characters. In studying willows we should bear in mind the following remarks of the distinguished English salicologist, F. BUCHANAN WHITE (Jour. Linn. Soc. **27**:346 [Rev. Brit. Willows]. 1890):

> Whilst all the parts of the plant are variable, some characters, on which a great deal of reliance has been placed, are so inconstant that they may, in many cases at least, be almost or quite ignored, though in other instances they are really of importance. Familiarity with the species can alone teach the student what are the points on which he can depend.

At present it is impossible to interpret properly certain forms because we do not yet know the degree of variation of the species in question. There are, I am convinced, many hybrids, and the fact that has been recognized by all the leading salicologists in Europe "that willows hybridize with the greatest facility adds," as WHITE (*loc. cit.*, p. 340) says, "immeasurably to the intricacies of the study." Here in America we are only just beginning to get a better understanding of the taxonomy, variation, and distribution of the numerous willows, and everyone who attempts to further our knowledge of them ought to be lenient in his criticism of those interested in this study.

It is not without hesitation that I propose the following varieties of *S. anglorum*, but I am encouraged by the fact that such a keen observer as Professor M. L. FERNALD, who has collected most of the material of the new forms and to whom I wish to express my gratitude, agrees with my treatment of them.

S. ANGLORUM var. **kophophylla**,[4] nov. var.—Frutex prostratus ramis subterraneis ad ultra 1 cm. crassis, ramulis repentibus pl. m.

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[4] The name is derived from κωφός, blunt.

elongatis, fructiferis ut videtur tantum ascendentibus; ramuli novelli sparse, rarius subdensius pilosi, vulgo citissime glabrescentes, in sicco nigrescentes vel flavescentes vel hornotini autumno ut annotini purpurascentes, ad 2 mm. crassi, annotini biennesque purpurei badiive, interdum ut vetustiores pl. m. pruinosi, vetusti crassiores pl. m. nigrescentes. Gemmae ovatae, obtusae, glabrae, badiae, saepe leviter pruinosae, ad circ. 5 mm. longae, floriferae ut videtur obovatae, obtusiores. Folia adulta satis chartacea, inferiora minora variabilia, superiora majora vulgo late ovalia, ovato-rotundata, obovata, late elliptica ad orbicularia, apice rotundata vel satis breviter acuta, interdum brevissime plicato-apiculata, basi late cuneata, rotundata ad subcordata, 1.5:1.2 vel 2.3:1.8 ad 3.5:2.5–2.8 cm. magna, interdum ovato-rotunda ad 3.5 cm. longa et 3 cm. lata, margine integerrima, rarius partim sparse subdenticulata, vulgo parce (juniora densius) ciliata, superne ut videtur tantum novella pl. m. sparse villosula et in costa pilosula, cito glabra, saturate et vivide viridia, stomatifera, costa subimpressa nervis lateralibus subprominulis et etiam graciliter reticulata, subtus valde discoloria, glaucescentia, pruinosa, initio magis quam superne sericeo-villosa sed etiam (infimis minoribus exceptis) cito glabra, costa nervisque primariis utrinque 5–8 pl. m. flavescentibus vel brunnescentibus elevato-nervata et graciliter sed distincte reticulata. Petioli longitudine satis variabiles, superne sulcati, initio pl. m. pilosi, dein glabri, 2–14 mm. longi. Stipulae nullae vel raro evolutae, lineari-lanceolatae, glanduloso-denticulatae, subglabrae, visae vix ultra 2 mm. longae. Amenta satis serotina, ramulos foliatos 0.5–2(–2.5) cm. longos pl. m. pilosos terminatia, cylindrica, rhachi villosa; mascula (no. 3232) 1–2 cm. longa et circ. 8 mm. crassa; bracteae obovato-oblongae ad late obovatae, apice obtusae vel retusae, omnino fuscae vel apicem versus atrae (in vivo pl. m. purpurascentes?), utrinque satis longe sericeo-pilosae; stamina 2; filamenta libera, glabra, bracteis demum duplo longiora; antherae parvae, ellipsoideae, ut videtur violaceae; glandulae 2 (vel interdum 1), ventralis ovato-rectangularis, truncata, integra (semper?), bractea duplo brevior, dorsalis (3232) duplo minor et angustior (in no. 510 nulla); amenta feminea sub anthesi ut videtur circ. 1–1.5 cm. longa et 0.6 cm. crassa, satis densiflora, fructifera

ad 3.5:1.4 cm. magna; bracteae ut in floribus masculis; ovaria sub anthesi ovoideo-oblonga ellipticave, sessilia vel subsessilia, albo-vel griseo-villoso-tomentosa; styli distincti, vulgo apice bifidi, rarius subbipartiti, stigmatibus oblongis bifidis 2–2½plo longiores; glandula 1 ventralis, anguste ovato-conica, truncata, integra vel ut videtur pleraque bifida bipartitave, bractea subduplo brevior fructus elliptico-conici, circ. 7 mm. longi, fere sessiles, ut ovaria vel minus dense pilosa (interdum in forma porro observanda [nos. 61 et 62] fere glabri), valvis apertis paullo recurvatis.

TYPE LOCALITY.—Western New Foundland, Bay of Islands, northeastern region of the Blomidon Mountain.

RANGE.—Western New Foundland, Bay of Islands and Bonne Bay, and western Gaspé Peninsula, Mt. Albert.

SPECIMENS EXAMINED.—Western New Foundland, northeastern region of the Blomidon ("Blow-me-down") Mountains, serpentine tableland, alt. about 550 m., July 24, 1910, *Fernald* and *Wiegand* (no. 3231, f.; G.; "prostrate near melting snow"; no. 3232, m., 3233, fr. type; G.; "prostrate"); Blomidon Range, July 3–5, 1911, *C. S. Stewart* (no. 29, st.; G.); Bonne Bay, serpentine tableland, alt. about 380 m., August 27, 1910, *Fernald* and *Wiegand* (nos. 3227, 3228, fr.; G.)—Gaspé Peninsula, Mt. Albert, deep ravine near snow, July 23, 1881, *J. A. Allen* (m., f.; G.); north slope of Allen's ravine, on hornblende schist, July 26, 1906, *Fernald* and *Collins* (nos. 501, 503^b, f., 507, fr.; G.); on wet serpentine slopes, July 23, 1906, *Fernald* and *Collins* (nos. 508, f., 510, m., 514, fr.; G.); brookside near permanent water, alt. 700 m., August 13, 1905, *Collins* and *Fernald* (no. 60, fr.; G., N.; partim fructibus satis glabrescentibus); dry serpentine barrens, 1000–1050 m. alt., August 9, 1905, *Collins* and *Fernald* (no. 62, fr.; G.; partim fructibus glabratis ut in no. 60).

In its rather short and dense catkins, at the base not or hardly loosely flowered, this variety approaches typical *S. anglorum*, but differs in its firmer, more rounded, and soon glabrous leaves and the glabrate twigs, in which characters it comes near to the following varieties. There is also no. 3235 of *Fernald* and *Wiegand*, collected at the same time as no. 3231 "from near sea level to serpentine tableland, alt. about 550 m." as a prostrate shrub. It occurs, according to the specimens in Herb. G., with the rounded leaves of the typical *kophophylla*, and also with more acute, lanceolate leaves, and both forms seem not to possess stomata in the upper leaf surface. So far as we know at present, there is no *S. cordifolia* in the Blomidon Mountains, and therefore this form cannot be connected in any way with *cordifolia* var. *Macounii* (Rydbg.) m. (see my second article). It certainly needs further observation. No. 3234, collected by *Fernald* and *Wiegand* in the northeastern region of the Blomidon Range, on serpentine tableland, about 550 m. alt., July 24, 1910

(fr.; G.), much resembles *S. cordifolia*, but I found stomata in the upper side of the leaves. We do not know enough of the willows of this range to be able to determine this form properly.

S. ANGLORUM var. **araioclada**,[5] nov. var.—Frutex ut sub var. *kophophylla* descriptus sed sequentibus signis distinctus: folia adulta satis tenuiter papyracea, minora inferiora obovalia, obovato-oblonga vel ut majora superiora ovalia, elliptica, ovato-elliptica, obovato-elliptica vel rarius obovato-lanceolata, apice vulgo magis obtusa vel rotunda quam acuta, raro retusa vel subito plicato-acutata, basi rotundata ad late cuneata, rarius sensim attenuata, margine integerrima, minimis exceptis 1.5:1 vel 3:2 ad 4:2.7 vel 5:2.9 cm. vel angustiora acutiora ad 4:1.8 cm. magna, superiora vulgo abinitio glaberrima; petioli interdum ad 10 mm. longi; stipulae rarissime evolutae, minimae, lineari-lanceolatae, caducae; amenta fructifera ramulos foliatos ad 4 cm. longos terminantia; mascula 1.5–2.5:1 cm. magna, minus quam in typo sericea; bracteae longe sed satis laxe sericeae; glandulae 2–1; feminea sub anthesi ad 3.5:1 cm. magna, fructifera vulgo 3.5–5.5 cm. longa et 1.8 cm. crassa, basim versus vulgo distincte laxiflora; bracteae interdum quam in masculis oblongiores sed saepissime densius sericeae, extus ad apicem interdum partim glabrescentes; ovaria ovoideo-oblonga, griseo-villoso-tomentosa, sessilia vel subsessilia; styli distincti, integri vel apice breviter bifidi, quam stigmata oblonga bifida vix duplo (rarius in floribus valde juvenilibus fere 2½plo) longiores; glandula ut in typo longa, pl. m. anguste conica, bractea duplo brevior; fructus ovato-conici, maturi ad 7–8 mm. longi pedicello subnullo vel brevi glandula ⅓ ad 2plo breviore excluso, laxius quam ovaria villoso-tomentosi, fulvi.

TYPE LOCALITY.—Gaspé Peninsula, north slope of Mt. Albert.

RANGE.—Gaspé Peninsula and the Selkirks and Rocky Mountains in British Columbia, Asulkan Valley, and in Alberta, near Laggan and Jasper Park.

SPECIMENS EXAMINED.—CANADA: Quebec, Gaspé County, Mt. Albert, deep ravine near snow, alt. 810 m., August 2, 1881, *J. A. Allen* (m.; G.; amentis parvis ovatis, glandula dorsali nulla, forma porro observanda); alt. 750–1050 m., July 26, August 2, 1881, *J. A. Allen* (m., f.; G. ex herb. Bebb;

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[5] Derived from ἀραιός, slender, and κλάδος, branch.

amentis parvis); head of Allen's ravine, August 8–15, 1905, *Collins* and *Fernald* (fr. im.; G.); north slope of same mountain, on hornblende schist, July 26, 1906, *Fernald* and *Collins* (no. 500, m. paratype; G.; 501^{a}, f.; G.; 503, 503^{a}, f. adult., 505, f. type; G.); July 20, 1906, *Fernald* and *Collins* (no. 506, fr.; G.); on wet serpentine slopes, July 23, 1906, *Fernald* and *Collins* (no. 510^{a}, m.; 514, fr.; G.).—BRITISH COLUMBIA: Selkirk Mountains, Rogers Pass, alt. 1350 m., July 31, 1890, *J. Macoun* (no. 18^{a}, f.; N.); Asulkan Valley, Glacier, alt. 1590 m., *J. G. Jack*, August 14, 1904 (fr.; A., G.); same place and date, *A. Rehder* (fr.; A.; both specimens identical with those like no. 506 from Gaspé).—ALBERTA: Lake Agnes near Laggan, August 11, 1904, *A. Rehder* (m., f.; A.; forma incerta quamvis ad *S. petrophilam* spectans); slopes of ravine on Mt. Aylmer, alt. 2250 m., August 4, 1899, *W. C. McCalla* (no. 2248, m., f.; Cor.); mountains above Lake Louise, alt. 1800–2400 m., July 21, 1907, *F. K. Butters* and *E. W. D. Holway* (no. 262, f.; N.; forma quasi ad *S. petrophilam* transiens sed foliis magis quam in hac specie discoloribus); Lake Louise, July 22, 1904, *J. Macoun* (no. 68883 O., fr.; N.); Fitzhugh Mountain, near Jasper Park, August 1917, *J. M. Macoun* (nos. 95379, 95397, 95398, 95401 O., fr., m.).

This peculiar variety differs from the type chiefly in its less pubescent, mostly much more elongated, and yellowish twigs, in its almost glabrous young leaves, and in its aments which, on an average, are longer and thinner, at least much more loosely flowered toward the base. It is, apparently, closely connected with var. *kophophylla*, which as a whole has firmer leaves and denser and shorter catkins, but in its glabrous character comes nearer to var. *araioclada* than to the typical *anglorum*. See also my remarks under the following form.

S. ANGLORUM var. **antiplasta**,[6] nov. var.—Frutex habitu ramulisque ut in var. *araioclada;* folia adulta chartacea, anguste ovalia, elliptico-oblonga, anguste obovato-oblonga, interdum oblanceolata, rarius elliptica vel obovato-elliptica, utrinque pl. m. acuta, raro rotundata, saepe apice breviter plicato-acuminata, vulgo 1.5–2.5 cm. longa et vix ultra 1 cm. lata, maxima ad 3:1.3–1.5 (rarius 1.8) cm. magna, integerrima vel interdum basim versus obsolete parce denticulata, superne subtusque ut in var. *araioclada* sed nervis lateralibus vulgo ut in *petrophila* angulo acutiore a costa abeuntibus et magis versus apicem currentibus; petioli graciles, 2–8 mm. longi, vulgo sparse pilosi; amenta cylindrica, sub anthesi satis brevià et tenuia, vulgo sublaxiflora, ramulos laterales in masculis vix ad 1 cm. longos ceterum ut in *araioclada* terminantia,

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[6] Derived from ἀντίπλαστος, similar.

rhachi parteque nudo pedunculi pl. m. villosa; mascula vix ad 1.5:0.7 cm. magna, bracteae et cetera ut in *araioclada*, glandula dorsalis (an semper?) nulla; feminea sub anthesi 1–2:0.5–0.7 cm. magna, fructifera vix ad 3 cm. longa et 1.2 cm. crassa, bracteae ut in masculis; ovaria ovoideo-oblonga, pl. m. sessilia; styli distincti, saepe apice breviter bifidi, stigmatibus brevibus oblongisve paullo vel ad 2.5plo longiores, glandula ut in varietate precedente; fructus ovato-conici, subsessiles, ad 6 mm. longi, laxius quam ovaria villoso-tomentosi vel anni praeteriti subglabrescentes.

TYPE LOCALITY.—Gaspé Peninsula, serpentine slopes of Mt. Albert.

RANGE.—As above.

SPECIMENS EXAMINED.—CANADA: Quebec, Gaspé Peninsula, Mt. Albert, serpentine slopes, July 23, 1906, *M. L. Fernald* and *J. F. Collins* (no. 509, f., fr., type; G.); exposed serpentine barrens, alt. 1000 m., August 9, 1905, *Collins* and *Fernald* (no. 61, m., f.; G., N., O.); sheltered mossy knolls, August 10, 1905, *Collins* and *Fernald* (no. 61^a, f.; G., N., O.; a precedente nonnisi petiolis vulgo longioribus differe videtur); on wet serpentine slopes, July 23, 1906, *Fernald* and *Collins* (no. 511, fr.; G.; forma gracilis juvenilis, habitu *S. petrophilae* valde similis); north slope of same mountain, on hornblende schist, July 26, 1906, *Fernald* and *Collins* (no. 504, f. defl.; G.; forma satis vegeta, ramulis elongatis, foliis pl. m. plicato-acuminatis).

At first sight this variety much resembles *S. petrophila* in its habit, the shape of the leaves, and the yellowish color of the young twigs, but the leaves are of a deeper green on the upper surface and much paler and glaucescent on the lower surface, and do not differ in this respect from any other form of *S. anglorum*. It is, however, much easier to distinguish herbarium specimens of both species than to express the differences in exact words. The two species meet each other in the Rockies of Alberta and British Columbia, and there are also certain forms in northern Montana, and even in Wyoming which at present I am at a loss to determine. Some of them may represent hybrids between *S. petrophila* and other species with which I am not yet sufficiently acquainted.

3. S. PETROPHILA Rydbg., in Bull. N.Y. Bot. Gard. **1**:268. 1899, is the species which seems to be nearest related to *S. anglorum*. It was first described by ANDERSSON (DC., Prodr. **16**^{2}:287. 1868) as *S. arctica petraea* from specimens collected by *E. Bourgeau* "in summo Rocky Mountains." I have seen a photograph of the type at Kew and a cotype in the Gray herbarium. Both specimens bear the label of PALLISER's Brit. N. Am. Expl. Expedition, with the printed indication "Rocky Mountains" and "coll. E. Bourgeau

1858"; and upon them is written "*Salix arctica* R. Br. *subalpestris* And. (forte n. sp.)." ANDERSSON apparently changed the varietal name later to *petraea*. The Kew sheet also bears, in the lower left corner, the inscription "*Salix herbacea*. Montagnes rocheuses Palouse près les Glaciers. 18 août 1858." According to MACOUN (Cat. Canad. Pl. preface, p. viii. 1883), BOURGEAU "spent some time, in August 1858, in the Bow River Pass and the adjacent mountains" in Alberta. *S. petrophila* differs from *S. anglorum* chiefly in the color of the rather pale or grayish green leaves, which are not distinctly paler and never whitish beneath. The differences indicated by RYDBERG between the two species are of no value, because his *S. anglorum* is mostly *S. groenlandica*. As I have already said, there are some forms in the northern habitat of *petrophila* which I have not yet been able to interpret properly. So far as I can judge by the specimens before me, the species ranges from about 52° N. latitude in southwestern Alberta and southeastern British Columbia through western Montana, northeastern Wyoming, and central Colorado to the Truchas Peak in northern New Mexico. I have not seen specimens from Washington and it is not mentioned in PIPER'S Flora. In eastern Oregon I know only of two localities. From Utah and Nevada I have seen very little material, and in California it is found in the Sierra Nevada from Sierra County to Tulare County.

In western Nevada and the Californian Sierra, *S. petrophila* is mostly represented by a form which has been described as *S. caespitosa* by KENNEDY (Muhlenbergia **7**:135, *pl. 9*. 1912). Through the kindness of Professor C. W. LANTZ I have seen the type, which is preserved in the herbarium of the Agricultural Experiment Station at Reno. It was collected by the author on Mount Rose, Washoe County, Nevada, August 17, 1905 (no. 1173, fr.). It differs from typical *petrophila* in the more copious pubescence of the upper leaf surface, the acuter leaves, and the very short style. The last character seems very variable, and the type material before me consists only of fruits with withered styles and stigmas. Nevertheless, I am inclined to use the name *caespitosa* for a variety which seems to be the prevailing form in the western part of the range of *petrophila*, and this var. **caespitosa** (Kennedy), nov. var., may be distinguished by its foliis utrinque acutioribus apice subacuminatis superioribus superne (saltem in parte) satis villosis, subtus vulgo glabris ad 3.5:1.3 cm. magnis, amentis femineis (immaturis) interdum ad 6:1.3 cm. magnis basi valde laxifloris longe pedunculatis. The most extreme form of this variety has been collected by *Hall* and *Chandler* on Mount Goddard, Fresno County, California, July 24–26, 1900 (no. 685, m., f.; G.); and I refer to it also a specimen collected by *F. W. Congdon* on Mount Dana, Mono County, California, August 27, 1895 (m., fr.; N.).

It may be mentioned here that *S. cascadensis* Cock. (*S. tenera* And., non A. Br.) is regarded as very closely related to ***petrophila*** by RYDBERG, or as "perhaps only a variety" of it by BALL. I prefer to place it in a different group next to *S. phlebophylla*, and I shall speak of it later.

There are three more willows, which, in my opinion, should be included in the same group with *S. arctica*, namely *S. stolonifera* Cov., *S. ovalifolia* Trautv., and *S. groenlandica* Ldstr. The first two have been well treated by COVILLE (1901), and need only a few remarks, while the history and taxonomy of the last ought to be explained in detail.

4. S. STOLONIFERA Coville, in Proc. Wash. Acad. Sci. **3**:333. *pl. 41. fig. 1* (Willows of Alaska). 1901, "is a species of eastern Alaska, in the glacier region from Yakutat Bay to Glacier Bay and Lynn Canal." RYDBERG (1899) mentioned this species under the name of *S. unalaschensis* "Cham. Linnaea **6**:539." As COVILLE has explained, CHAMISSO did not propose such a species, but merely describes a "*Salix* unalaschcensis, multis cum *arctica* Pall. conveniens, pluribus ab illa abhorrens, nulli nostrarum propius accedens," to which he did not give a specific name. His form from Unalaska is the same as *S. ovalifolia* Trvt., and ANDERSSON has already mentioned in the Prodromus "*S. unalaschkensis* Chamisso" among the synonyms of TRAUTVETTER's species. COVILLE describes the ovaries as "smooth or with some traces of pubescence toward the apex," and he regards the glabrous form as the typical and common one. I think it best to propose a f. **subpilosa,** f. nov., fructibus pl. m. interdum satis dense pilosis, because such forms resemble somewhat *S. arctica*, especially when the old fruits have lost the

style. The leaves, so far as I can see, always possess stomata in the upper epidermis, as is the case with typical *S. stolonifera*, while they are wanting in the leaves of typical *S. arctica* and *S. ovalifolia*. The length of the style and the rather long linear stigmas seem to be the best characters to distinguish *S. stolonifera* from the other species of this group. "The characteristic of the production of slender leafless, subterranean branches or stolons" is not always clearly seen on herbarium specimens, and the presence of such stolons may possibly be detected in other related species.

5. S. OVALIFOLIA Trautvetter in Nouv. Mém. Soc. Nat. Mosc. **2**:306, *pl. 13* (De Salic. Frig. Kochii). 1832.—*S. myrtilloides* forma 4 Chamisso in Linnaea **6**:539. 1831.—*S. unalaschkensis* Chamisso ex Andersson in Öfv. K. Vet.-Akad. Förh. **15**:130. 1858.—*S. rotundata* Rydberg apud Macoun, List Pl. Pribilof Islands in Jordan, Fur Seals N. Pac. **3**:571. 1899, non Forbes 1829.—*S. cyclophylla* Rydberg in Bull. N.Y. Bot. Gard. **1**:275. 1899, non Gandoger 1882.—The type locality of the species is Cape Espenberg in the Kotzebue Sound. Its range extends from the Bering Strait, where it is probably also found on the Siberian Coast,[7] northward to Point Barrow and Martin Point, where it has been found by *F. Johansen*, July 30, 1914 (no. 136^b or 93484 O., fr.); and southward to the Pribilof and Aleutian Islands and the Alaskan Peninsula, but it has also been collected on Kodiak Island, and to the eastward as far as Yakutat Bay. The typical form has glabrous ovaries and fruits; there are, however, specimens with loosely pubescent capsules collected by *Trelease* and *Saunders*, St. Paul Island (no. 3442, fr.; M.), which may represent the var. *pubescens* And. (DC. Prodr. **16^2**:291. 1868). This is described as being distinguished by "capsulis tenuiter hirsutis griseo-pubescentibus petiolis et foliis basi longius hirsutis." As no type is given, I cannot decide whether ANDERSSON's variety is identical with this specimen.

Some other specimens which COVILLE has cited as typical *S. arctica*, while RYDBERG took them for *S. diplodictya* Trautv., should be discussed. The last species has been described, as I have explained, as having the leaves green and glossy on both sides, and it has certainly nothing in common with the forms in question. These specimens seem to represent a form somewhat intermediate between typical *S. ovalifolia* and typical *S. arctica*. It may be characterized briefly as follows: ab *ovalifolia* satis diferre videtur foliis amentisque majoribus, floribus masculis tantum (an semper?) glandula ventrali instructis, ovariis satis pubescentibus etiam fructibus tenuiter vel partim (fere ut in var. *pubescente* supra) pilosis sed non distincte glaucescentibus; ab *arctica* praecipue recedit foliis minoribus pl. m. rotundatis vel obovato-rotundis, amentis parvioribus, fructibus minoribus (perfecte maturis non visis) pl. m. glabrescentibus vel partim glabris. I do not want to propose a new name for this form, because it needs further observation, but it is by no means identical either with *S. ovalifolia pubescens* or with *arctica*. It may be referred provisionally to *S. ovalifolia* var. *subarctica* Lundström in Nov. Act. Roy. Soc. Sci. Upsala III. 1877. p. 41, where the following characters are given: "*β, subarctica* nob. capsulis pubescentibus; foliis majoribus, subtus parce villosis." As I have said, the forms described by LUNDSTRÖM cannot be fully understood until his type material is examined.

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[7] Lg. C. WRIGHT in 1853–56 on Arakam Island. Those specimens are distributed as *S. uva-ursi*, but agree well with *S. ovalifolia* except that the fruits are not glaucous.

There remains another arctic form which I should have regarded as not separable from typical *S. ovalifolia* but for the fact that I found stomata in the upper leaf epidermis in most of the specimens cited later. So far as I can judge by the rather scanty material before me, this variety, for which I propose the name var. **camdensis,** var. nov., seems chiefly to differ from *S. ovalifolia* in the following respects: foliis nondum perfecte evolutis minoribus vel oblongioribus elliptico- vel ovato-oblongis vel oblanceolatis apice acutis vel obtusis basi acutis vel pl. m. rotundatis vix ultra 1.5 cm. longis et 1 cm. latis in epidermide superiore vulgo pl. m. stomatiferis adultis textura tenuiore et subtus minus distincte reticulatis, petiolis saepe quam gemma brevioribus, amentis masculis submajoribus ad 1.5:1 cm. magnis, fructiferis subminoribus ad 1.5 cm. longis et 1.2 cm. crassis.

I examined the following specimens: Alaska, Camden Bay, Collinson Point, July 17, 1914. *F. Johansen* (no. 116 or 93482 O., fr., type in O.); June 1914. *F. Johansen* (no. 44ᵃ or 93807 O.; f.; stomata non visa; no. 44ᵇ or 93806 O., m.); Kongenevik, July 1914. *F. Johansen* (no. 82ᵃ or 93805 O., m.

syntype; no. 82^b or 93804 O., fr.; stomata superne in foliis non visa); west of Martin Point, July 30, 1914, *F. Johansen* (no. 136^a or 03483 O., st.; folia superne stomatibus numerosis instructa breviter petiolata, forma porro observanda).

Dr. FRITS JOHANSEN has been so kind as to give me the following information regarding this variety: "Nos. 44a, b, Collinson Point. This willow grew on more bare, gravelly tundra near the beach (transition region to the latter), in patches of several plants. Its growth was very prostrate and depressed (among stones and vegetation), with the stems and branches lying very close to the ground and spreading widely, so that only the catkins showed up from a little distance. Especially the subterraneous parts (roots and stem parts) were less extensive and spreading than with those found at Kongenevik, Alaska (see below); probably because they did not grow on sand dunes as is the case at the former place.—Nos. 82a, b, Kongenevik. The collecting place was where the seashore (beach) through low sand dunes goes over into the more typical tundra behind. On these sand dunes the vegetation is very characteristic and consists almost exclusively of *Elymus*, *Carex*, *Salix*, *Chamaerium*, etc.; each species spreading (both above and under the ground) over large patches (areas) and dominating more or less to the exclusion of the other species. This *Salix* seemed to be very prostrate, but the larger part of each plant is buried in the sand, so that only the leaf and catkin-carrying branch parts (outer third) protruded. It was mostly large plants widely spreading (both roots and stems); the branches often having the form of long "runners" intersecting the sand rhizome-like in all directions. The sand-covered parts of the branches were without leaves or catkins and pale (white-yellow). When growing in less sandy soil the growth is naturally more condensed (see above under Collinson Point). The plants were in full bloom in the end of June.—Nos. 136a, b, Martin Point. The collecting place was a sandy gravel spit of slight elevation, with the sand dunes less pronounced than at Kongenevik. Vegetation rather scattered and in patches, except around the several ponds and the big lagoon between the sand spit and the mainland behind. On sandy places the vegetation was much like that at Kongenevik, with *Honckenyia* taking the place of *Chamaerium*. As the character of the spit was somewhat intermediate between the beach regions at Collinson Point and at Kongenevik, so did also the growth of the *Salix* in question resemble those of the same species from both of the foregoing places. At the time of collecting the plants had dropped ♂ catkins and had unripe ♀ catkins."

6. S. GROENLANDICA Lundström, Nov. Act. Reg. Soc. Sci. Upsala III. 1877. p. 36.—*S. arctica* Liebmann, Fl. Dan. XIV. fasc. 42:7, *pl. 2488*. 1849, non Pall.—*S. arctica* γ, *Groenlandica* And. in DC., Prodr. **16**^{2}: 287. ut videtur excl. forma 6 *pusilla*.—ANDERSSON

based his var. *groenlandica* on "*S. arctica* Fl. Dan. t. 2488." and he distinguished 6 forms: (1) *hebecarpa*, which is nothing but the type; (2) *lejocarpa*, with glabrous ovaries; (3) *latifolia*, which probably only represents a vigorous form with "foliis orbiculato-ovalibus"; (4) *angustifolia*, a mere form with "foliis lanceolatis"; (5) *macrocarpa*, which is nothing but the typical plant with normal big aments; and (6) *pusilla*, which I cannot interpret because the description ("fruticulus vix digitalis, foliis 1–3 lin. longis densissime confertis. *Salici retusae serpyllifoliae* analoga") is insufficient, and ANDERSSON does not cite a type or any locality for it. The description and figure given by LIEBMANN are quite sufficient to understand what form is meant, and it is rather surprising that this well marked species could be misunderstood by later authors. LUNDSTRÖM did not say much about it, because he was dealing with Asiatic and European forms, and only wanted to separate it from the related species. LANGE (Consp. Fl. Groenl. **1**:108. 1880), in adding his var. "*minutifolia* And. mscr." to those already described by ANDERSSON (but omitting f. *macrocarpa*), referred *S. arctica* Br. (*S. Brownei* Ldstr.) as a synonym to *S. groenlandica*, and seems to have misunderstood BROWN's plant. RYDBERG, in his turn, as I have said, mixed the real *S. groenlandica* with his *S. anglorum*, and gave the name *groenlandica* to specimens of the latter species and to several forms of different origin. In my opinion the true *S. groenlandica* may easily be recognized by its glabrous leaves, which are shining dark green and without stomata above and distinctly glaucescent beneath, the margin being entire or often more or less glandular denticulate, by its large aments which measure from 5:1.2 to 10:1.6 cm. in fruit, and by its distinctly pediceled ovaries, which bear a rather thin and short silky pubescence even when young and possess a short and broad gland of about half the length of the pedicel. The shape of the ventral gland, which is the same in both sexes, differs much from that of the other species of this group where, as a rule, it is oblong or ovate-conical and longer than the pedicel. The thin pubescence of the ovaries and fruits, which are often almost glabrate or entirely glabrous in var. *lejocarpa* (And.) Lange, gives them a different aspect from the tomentose capsules of *S. arctica*, *S. anglorum*, or

S. petrophila. In the size of the fruiting aments *S. groenlandica* is next to vigorous forms of *S. arctica* and to *S. arctica* var. *subcordata.*

The type of *S. groenlandica* has been collected by VAHL "in locis humidis Groenlandiae orientalis et occidentalis a limite maris ad alt. 200 pedum." I have not seen a specimen of VAHL's and no material from eastern Greenland. Judging by the specimens I have examined, its range extends from Disco Island (70° N. latitude) through the southern part of Baffin's Land westward to the Bathurst Inlet (about 109° W. longitude), and southward along the shores of the Hudson Bay through Ungava and Labrador to the western Gaspé Peninsula and the Port à Port Bay in western Newfoundland. There are also some rather uncertain and fragmentary specimens from the Lancaster and Jones Sound, and probably the habitat of *S. groenlandica* reaches its northern limit at about the 76th parallel. Other specimens have stomata in the upper epidermis of their leaves and may represent a different variety or be of hybrid origin; they need further observation.

ARNOLD ARBORETUM
JAMAICA PLAIN, MASS.

FECUNDATION AND FORMATION OF THE PRIMARY ENDOSPERM NUCLEUS IN CERTAIN LILIACEAE

MILDRED NOTHNAGEL

(WITH PLATES III–V)

Introduction

Between 1890 and 1902 many articles appeared on fecundation and double fertilization in the angiosperms. On the whole, the authors have dealt with the entrance of the male nuclei, their behavior within the embryo sac, their form, the union between the egg and male nucleus, and between the male and polar nuclei; but they have not investigated in detail the chromatin changes that occur from the time of contact of these nuclei to the completion of the first division.

In 1891 GUIGNARD (**6**) described the entrance of the so-called antherozoids into the sac, each accompanied by its centrosomes. One male nucleus became applied to the egg nucleus, each of which took on the resting condition and remained distinct for some time. While in this state the male nucleus enlarged and both the egg and the sperm nucleus flattened at the surface of contact, but with a distinct line of demarcation remaining between them for some time. Even after the nuclear membranes had disappeared, the contour of the two was traceable at the periphery. Later he distinguished, on opposite sides of the nuclear cavity, two groups of chromatin in the spirem stage. No drawings were made to show this. When the nuclear plate was formed, he asserted that one-half of the chromosomes were contributed by the egg and one-half by the sperm.

The process of fertilization in *Lilium Martagon* and *L. candidum* was described by MOTTIER (**13**) in 1898. In *L. Martagon* there was no complete fusion of egg and S-shaped sperm, the lack of which resulted in a failure to mature seeds. In the region of the two polar nuclei, which had not fused and which began disintegrating 96 hours after pollination, a nucleus, similar to the nucleus which united with the egg, was observed. *L. candidum* furnished material for normal fertilization. At the union of the egg and sperm, the latter was about the size of the former and both were in the resting condition, the chromatin being distributed in the form of a fine network. No boundary was observed separating the two elements at the point of contact, and the fusion that took place during resting condition was so complete at the close of fertilization that there was no visible distinction between male and female chromatin.

In 1904 MOTTIER (14) confirmed his earlier investigations, pointed out the S shape of the male nucleus, the fusion of the sexual nuclei in resting condition, the coming together of the two polar and male nuclei in *L. Martagon*, and the cause of the non-fusion. Although he stated that the sexual nuclei were in the resting condition at the time of fusion, he called attention to the chromatin of the sperm being more regular than that of the egg. It was also claimed that the nucleoli fused at fertilization.

One of the first reports of double fertilization was made by GUIGNARD (7) in 1899 for *Lilium Martagon*. In this species he observed the union of one of the male nuclei with one of the polar nuclei, followed by the union with the second polar nucleus. The chromatin of the two male nuclei, on account of being coarser, was distinguishable from that of the egg and polar nuclei with which they had fused. He also stated that he was able to recognize the triple origin of the secondary nucleus during the prophases, although no drawings were given.

NAWASCHIN (15), in the first report of double fertilization in *Lilium Martagon* and *Fritillaria tenella*, noted that the cellulose membrane surrounding the sexual apparatus was absorbed just previous to the entrance of the pollen tube, and that the spiral-shaped male nucleus entered the protoplasm of the sac. He concluded that the sperms took on various shapes under various conditions, and, as GUIGNARD had assumed, that they were motile. One sperm was found to enter the egg, the other to unite with the superior polar nucleus, and in both cases a complete fusion occurred after a certain period. The fusion of the superior and inferior polar nuclei took place after the male nucleus had united with the former. The triple fusion was followed in a short time by a division which preceded that of the egg.

In 1900 GUIGNARD (**9**) found that in some cases the polar nuclei, the upper one of which he said was analogous to the egg, fused before the entrance of the pollen tube, and that when the male nuclei entered the sac, they entered into fusion so quickly that, in some species, one rarely saw them free. In *Tulipa* he was able to follow the contour of the three nuclei entering into the fusion nucleus some time after their coming together, and even after the membranes had disappeared at their surface of contact.

As a result of investigations in various groups of angiosperms by GUIGNARD (**6, 7, 8, 9, 10**), NAWASCHIN (**15**), STRASBURGER (**17, 18**), and others at this time, it was generally concluded that double fecundation was normally found in angiosperms and that the uniting of the male nucleus with the polar nuclei was in the nature of a pseudo-fecundation whose function was to stimulate the formation of "albumen."

ERNST (**3**), investigating fertilization of *Paris quadrifolia* and *Trillium grandiflorum*, found that the two polar nuclei were fused before the male nucleus united with them, and at times a spirem was formed previous to the entrance of the sperm, showing that the male nucleus was not necessary to stimulate division. At other times the spirem was not formed until the three nuclei were fused, in which case he was unable to discern which part of the chromatin was contributed by the various nuclei. He also stated that it was not safe to rely upon the number of nucleoli found in the fused mass to ascertain whether fertilization had taken place or not. In the fecundation of the egg there was a complete blending of the substances, and at cross segmentation he failed to find the arrangement of the chromatin into two groups.

STRASBURGER (**17, 18**) used the terms generative and vegetative fertilization, the latter being applied to the triple fusion. The union of the sperm, either with the egg or with the polar nuclei, functioned as a stimulus.

In 1911 COULTER (**2**), after reviewing the literature on endosperm formation, stated that since endosperm may form without the fusion of the sperm or even of the second polar nucleus, these being simply supplementary, there seemed to be no reason why "there should be any hesitation in recognizing the endosperm as gametophyte." He concluded that "the product of such fusions is merely an undifferentiated tissue which practically continues the tissue of the gametophyte, that is, it is simply growth and not organization."

From 1902 to 1913 practically nothing new was published on the subject of fertilization. In 1913 BLACKMAN and WELSFORD (**1**) reported that the chromatin of the vermiform male nucleus was in a network, although not the network of a resting nucleus, this condition becoming more noticeable later on. At times they also noted that the chromatin of the egg might become threadlike just previous to fusion.

The most recent paper on fertilization is by SAX (**16**) in 1916 on fertilization in *Fritillaria pudica*, in which he noted that the vermiform sperm lay indented in the egg for some time before the membranes between them disappeared. The chromatin was in more or less of a network and the granules were of various sizes. When the membranes at the surface of contact broke down, the contents of the two nuclei mingled and were not distinguishable from each other. The spirem usually appears after this. Triple fusion was also complete and the resulting nucleus divided before that of the fertilized egg.

In none of these cases have the chromatin changes been carefully followed from the time of contact of the nuclei until the completion of the first division, the emphasis previously having been placed upon the actual coming together, the uniting, and the very earliest steps in division.

The process of fertilization and distribution of the chromatin contributed by the egg and sperm in *Pinus* and *Abies* has been carefully worked out by FERGUSON (**4, 5**) and HUTCHINSON (**12**), and it was with the desire that something of this nature should be done for angiosperms that the present investigation was undertaken.

Materials and methods

For fertilization of the egg, *Trillium grandiflorum* was used, the material being collected in damp woods along the Des Plaines River, northwest of Evanston, Illinois, from May 3 to May 26, 1916. The first collection was made at the time of pollination, although the pollen tube was not seen in the micropyle until two weeks later, while in the collection of May 26 dividing endosperm nuclei and second division of the fertilized egg were found for the first time. *Lilium Martagon*, collected from the garden of Indiana University, Bloomington, Indiana, in May 1916, 96 and 120 hours after pollination, was more favorable for the first division of the endosperm nucleus. The former material was killed and fixed in chrom-osmic-acetic acid 1–2 hours and then in chromo-acetic acid 24–36 hours, washed, dehydrated, and imbedded either from chloroform or xylol. *Lilium Martagon* ovaries were killed and fixed in chrom-osmic-acetic acid 24–36 hours, washed, dehydrated, and imbedded from chloroform. All sections were cut 12 μ thick and both modified triple and Heidenhain's iron-alum-haematoxylin were used for staining, the latter being more satisfactory for most stages, as the chromatin was more sharply differentiated.

Formation of the primary endosperm nucleus

For the development of the spirem and the first division of the endosperm nucleus, *Lilium Martagon* was found to be very favorable, as many dividing primary endosperm nuclei were found in the sacs of material killed 96 and 120 hours after pollination. Activity did not cease at the end of the first divisions, for as many as 12–16 nuclei were found in many sacs of the older material (fig. 29).

The sperm comes in contact with the polar nuclei before these two have fused, although they may be in contact or in close proximity (fig. 17). These three nuclei will usually be found in the center of the sac where just previous to the triple fusion the two polar nuclei were to be seen.

The chromatin of the egg can scarcely be said to be in a network, but rather to consist of strands which are more or less united (figs. 17, 18), that of the male nucleus being much coarser than that of the polar nuclei. When the sperm reaches the middle of the sac, it still has its curved or vermiform shape, while the contour of the polar nuclei may vary, sometimes being quite curved before coming together (fig. 17), but at other times only changing to this shape as pressure is exerted by contact. The three nuclei upon uniting may be variously twisted about each other, the male nucleus usually twisting more than the others and recognizable by its coarser chromatin strands (fig. 18). In fig. 18 the three nuclei as a whole present a more or less globular contour, although the nuclear membranes are still present at the surfaces of contact.

In *Trillium grandiflorum* the three nuclei, which unite to form the primary endosperm nucleus, are all alike in shape, it being impossible to distinguish the male nucleus from the two polar nuclei by its form or size (fig. 16). Since the mass of the three nuclei is so large, it is often impossible to find parts of all three nuclei in one section, and frequently only two will be visible (fig. 19). All three contain nucleoli, sometimes one, while at other times there are many. The chromatin strands thicken until they may be traced for a considerable distance (figs. 19, 20). While in some instances the membranes still separate the nuclei (fig. 20), at other times they are not visible, as in fig. 19; but, nevertheless, where the chromatin contributed by one nucleus leaves off and that of another begins is very easily seen.

Up to the period when the spirem has assumed its mature thickness, the separating membranes may not have entirely disappeared (fig. 21), and in some cases the three groups of spirems are plainly evident. From fig. 22 it could be concluded that a complete fusion or intermingling of chromatin had previously occurred, but such has not happened, for in the next section of this same primary nucleus parts of all three nuclei are seen (fig. 21). Even at this stage, before the complete breaking down of the separating membranes, segmentation has begun and spindle fibers are forming about the group. As far back as the coming together of the two polar nuclei and the sperm nucleus, a surrounding complex of fibers could be seen (fig. 18).

In fig. 21 the fibers have commenced to radiate out into the cytoplasm, followed after a short period by a complete segmentation of the spirems, resulting in three groups of chromosomes being scattered upon the three arms of the tripolar spindle, respectively (figs. 23, 24). As the tripolar structure gradually assumes the form of a bipolar spindle, the chromosomes, which were previously lying upon the third arm, are pulled into line with the other two groups, thereby forming a typical bipolar spindle (figs. 24, 25). The chromosomes now thicken and are typically arranged into the equatorial plate of the bipolar spindle; but even yet the third group of chromosomes is recognizable, as can be seen at the left in the group in fig. 25.

After this stage the chromosomes contributed by each of the polar nuclei and by the sperm nucleus are no longer distinguishable (fig. 26). No trace of such distinction is seen in early metaphase or later spindle phases. How the various chromosomes finally arrange themselves upon the spindle and their distribution could not be ascertained in this investigation. When the $3x$ chromosomes have gathered upon the equatorial plate of the bipolar spindle, each very much elongated chromosome splits longitudinally (fig. 26) preparatory to a typical equational division. No intermediate stages between early metaphase and early telophase were found. As the chromosomes reach the poles, they are somewhat shorter than when leaving the equator, and from the count, as seen in fig. 27, $3x$ chromosomes have passed to each pole.

In the third division of the endosperm nuclei of *Trillium grandiflorum* a peculiarity was noted. In one of the dividing nuclei there were still to be seen the three groups of chromosomes upon the spindle, each group consisting approximately of six chromosomes, or the haploid number. It is easily seen that there is a great similarity in appearance between this third division of the endosperm and the first division of the primary endosperm nucleus. A similar stage was observed in the second division of the endosperm nucleus of *Lilium Martagon* (fig. 29), showing in the upper dividing nucleus an appearance very similar to that seen in fig. 24. It was not determined how long endosperm division would continue in *Lilium Martagon*, as nothing older than 120 hours after pollination was collected.

Fertilization of the egg and its first division

Trillium grandiflorum furnished the best material for this phase of the investigation, as the later stages of the first division of the fertilized egg were not to be found in *Lilium Martagon* collected 120 hours after pollination.

In *L. Martagon* the chromatin of the egg and the sperm, at the time when the male nucleus lies coiled upon the egg, is similar in appearance to that described for the polar nuclei and the second sperm nucleus. The chromatin is in strands, that of the sperm being heavier than that of the egg (fig. 1). The sperm fertilizing the egg is very much smaller than the sperm uniting with the polar nuclei at the time of contact and not so vermiform (compare figs. 1 and 17). Fig. 2 illustrates a typical fertilized egg of ***Trillium grandiflorum*** just a little later in development than that of ***Lilium*** (fig. 1). In this later stage the chromatin is lumpy, the particles being larger in the sperm than in the egg, and the membranes separating the two nuclei are becoming very thin, so that it is difficult to distinguish them at all times. After this time these membranes are rarely to be found, although in some instances they persist for a longer period (fig. 4).

The chromatin gradually collects into larger groups, forming more or less broken threads connected with each other by fine anastomoses (figs. 3, 4). In many portions of the nucleus of this fertilized egg the parallel nature of some of these strands is quite conspicuous (figs. 3, 4). In some fertilized eggs, as for example in fig. 5, a more or less beaded, although discontinuous, spirem was noted. Even though the nuclear membranes which separated the egg and the sperm have disappeared, the chromatin that has been contributed by each of the two nuclei remains distinct (fig. 3). This condition is much more evident in some fertilized eggs than in others. The sperm at the period of union contains a much smaller amount of chromatin than the egg and throughout most of the subsequent stages this condition persists (figs. 3, 4, 9, 10, 12). During all this time the fertilized egg is growing in size and increasing the amount of chromatin. When the continuous spirem is first formed, it is quite thin (fig. 6), but as the prophase advances the chromatin thread thickens and shortens until a comparatively thick spirem results (figs. 6–12). Instead of one continuous spirem, two distinct spirems are usually to be seen within the single nuclear cavity, although located in different parts of the cavity (figs. 8–10). In some sections such differentiation is not visible (figs. 6, 7). The dotted lines *a–b* in figs. 9 and 10 separate the two spirems, one of which was contributed by the sperm, the other by the egg.

In spite of the fact that a nucleolus is not seen in the sperm when it unites with the egg, very small ones are found in later stages (fig. 3), and still later, in the spirem stage, a large nucleolus is frequently observed (fig. 9); but at the beginning of segmentation all traces of these nucleoli have vanished.

With the beginning of segmentation, the chromatin threads appear to contract, presenting the appearance of "the second contraction" of heterotypic mitosis (figs. 11, 12). Following this, the nuclear membrane surrounding the two groups disappears, leaving the massed segments lying free in the cytoplasm. Even now the two sets of chromosomes are separate (fig. 12), and to all appearances a spindle is formed about one group of chromosomes and the other set is pulled into the bipolar spindle, for, as late as in fig. 13, the chromosomes contributed by the sperm are distinct from those contributed by the egg. In each of the two groups (fig. 13) there are approximately six chromosomes, or the haploid number. The writer was unable to determine the arrangement of these two sets upon the equatorial plate, owing to lack of material for later stages. From the number of chromosomes seen at telophase and later divisions, each splits longitudinally at metaphase, so that twelve, the diploid number, pass to each pole.

Discussion

A very full, detailed account of fertilization in *Pinus* by Ferguson and in *Abies* by Hutchinson has been published; but a similar account is not to be found for angiosperms.

Ferguson (5) reports that in *Pinus* the chromatin of the egg is arranged in an interrupted reticulum, the network consisting of granules of various sizes in a colorless linin. When the contents of the pollen tube have been discharged into the egg, one of the male nuclei takes up a position on the concave side of the egg, this depression having been formed at the approach of the male nucleus. Gradually from each nucleus a spirem is formed from the respective chromatin material, at which period fibers arise in the region of the spirems and the nuclear membrane gradually fades away. At segmentation these two spirems give rise to two groups of chromosomes, but as they collect on the spindle this distinction is lost. Each chromosome splits longitudinally and each daughter nucleus receives the diploid number. When these daughter nuclei are preparing for second division, the chromatin collects into two spirems, the steps being very similar to those of the first division, and it is concluded that in all probability they come from the maternal and paternal source respectively, in spite of the fact that in the formation of the daughter nucleus the chromatin has appeared completely fused. Since the subsequent divisions were not followed, it could not be determined how long this dual nature persisted.

The account of fertilization in *Abies balsamea* by HUTCHINSON (**12**) varies somewhat from that of FERGUSON. The contents of the male nucleus pass into the nucleus of the egg, although the chromatin groups remain distinct, and later, when the two sets of spindle fibers are formed, two sets of chromosomes arise from the respective nuclei. These two spindle complexes unite and the chromosomes of the maternal parent pair with the chromosomes of the paternal parent, after which the fibers disappear. The members of each pair twist about each other, bend, and become transversely segmented at the bend so that there are $2x$ pairs in the fertilized egg. When the second set of fibers appears, the members of the pairs resulting from the transverse segmentation separate for the opposite poles.

HEATLEY (**11**) has described the development of the embryo sac of *Trillium cernuum*, in which the sac arises from the chalazal daughter nucleus of the megaspore mother cell, two megaspores only being functional. Each functioning megaspore divides twice to form the typically arranged 8-nucleate embryo sac.

In the present study it was not considered necessary to work out the development of the sac, and furthermore, no attempt has been made to determine the method of entrance of the sperms into the sac or their passage to the egg and polar nuclei. BLACKMAN and WELSFORD (**1**), ERNST (**3**), GUIGNARD (**6, 9, 10**), MOTTIER (**13, 14**), SAX (**16**), and STRASBURGER (**17, 18**) have reported on the earlier phase of fertilization, and on the whole have agreed. These same authors have also described in detail the coming together of the nuclei, their chromatin condition, and the breaking down of the nuclear membranes separating them, although GUIGNARD (**7–9**) differs somewhat from the others on the latter point, which will be spoken of later. By comparing these investigations with those of *Pinus* (FERGUSON **4, 5**) and *Abies* (HUTCHINSON **12**), it is apparent to the writer that the present knowledge of certain phases of fertilization in angiosperms is very scanty, especially as to the fate of the maternal and paternal chromatin.

ERNST (**3**) reports for *Trillium grandiflorum*, and a similar conclusion is reached by various authors for certain other plants, that there is a fusion of the polar nuclei previous to the entrance of the pollen tube; but in not a single case in either *Trillium* or *Lilium* has such a condition been found to exist, the polar nuclei always being distinctly separate, although usually in contact (figs. 16–19). Only a few cases of triple fusion were observed in *Trillium grandiflorum*, although all that were found appeared as illustrated in fig. 16.

BLACKMAN and WELSFORD (**1**), GUIGNARD (**7–9**), MOTTIER (**14**), and SAX (**16**) have noted that the male nucleus can be distinguished from the egg and from the polar nuclei both by its shape and the condition of the chromatin, since this substance is coarser in the male nucleus, and at times assumes almost a spirem condition previous to fusion. The sperms have been found not always to retain their S or curved form, for in *Trillium* the male nucleus could not be distinguished from the polar nuclei, either by its size or countour (fig. 16).

The three nuclei (superior and inferior polar nuclei and male nucleus) of *Lilium Martagon* become very much twisted about each other very soon after coming in contact (fig. 18), and even previous to this the polar nuclei may have lost their globular form (fig. 17), although the writer failed to find any mention of this in previous accounts. The fibers appear early about the nuclear complex of *Lilium* and gradually merge into the cytoplasm, as FERGUSON (**4, 5**) has reported for the fertilized egg of *Pinus*. The chromatin is in fine strands and not in a network, as GUIGNARD and MOTTIER have stated. The number of nucleoli in each nucleus may vary from one to several, and in some specimens there are none. As SAX (**16**) has said for *Fritillaria*, at the time of contact the chromatin is threadlike, with large irregular pieces of chromatin scattered throughout.

In many instances the separating nuclear membranes are still to be seen when the chromatin has been transformed into a comparatively heavy spirem (fig. 20), and in some instances at the beginning of segmentation fragments of it still remain (fig. 21). In cases where the separating nuclear membranes do disappear early, the limits of the nuclei are readily followed (fig. 19). GUIGNARD (**7**), in his first report of double fecundation, says that the chromatin of the sperm enters into more or less of a spirem before fusion with the two polar nuclei, after which, at times, he is still able to recognize the triple origin of the secondary nucleus of the sac. None of his drawings are later than fig. 18 of the writer, and apparently the chromatin is in the same condition. In a later paper (**8**) he describes a similar condition in *Narcissus*.

In *Fritillaria*, SAX (**16**), after stating that the chromatin of the male nucleus frequently passes into a spirem previous to the breaking down of the separating membranes, and in some few instances observing the beginning spirem in the polar nuclei, concludes that there is a complete fusion of the chromatin contributed by the three nuclei, and that this is further proved by finding no incomplete fusions in later stages.

In not a single specimen showing the formation of the primary endosperm nucleus was the writer unable to distinguish between the chromatin of the various nuclei that have contributed to this nuclear complex. From the view obtained in fig. 22 it could readily be concluded that a complete intermingling of chromatin has previously occurred, but when the next section of the same primary endosperm nucleus is examined (fig. 21), such a conclusion is seen to be groundless.

Whether or not the separating nuclear membranes have entirely broken down by the time of segmentation, the spirems remain distinct, and, following segmentation, three groups of chromosomes collect upon the three arms of the tripolar spindle (figs. 23, 24). In none of the literature examined has such a stage been shown or reported, for, if such had, the idea of complete fusion or intermingling of chromatin material could not have been adhered to up to the present time.

Since the chromosomes are very long and quite numerous (36), the writer was unable to follow definitely their final arrangement upon the bipolar spindle. From the appearance of fig. 25 it seems that the group on the right side of the equatorial plate might be the group that has been pulled into line. Soon after this each chromosome splits longitudinally, as FERGUSON (**4, 5**) has reported for *Pinus*, and all trace of the individuality of the groups is lost for a time.

It has been generally understood that in *Lilium Martagon* fusion and subsequent divisions did not occur unless the top was cut off from the bulb; but in the plants used in this investigation, in which this was not done, the ovaries showed many dividing endosperm nuclei and the sacs were in good condition (fig. 29). In *Trillium grandiflorum* in a sac of four dividing endosperm nuclei (fig. 28), and in *Lilium Martagon* in a sac of two dividing nuclei (fig. 29), as described previously, three groups of chromosomes are seen on the spindle. This corresponds to the condition of the second division of the oosphere, as FERGUSON (**4, 5**) has reported for *Pinus*, in which she notes that the second division is like the first, there being two spirems.

Figs. 28 and 29 distinctly show the three groups, and if such a condition is normal the question arises whether the male and female chromatin remaining distinct is the cause of the mottled appearance of some hybrid endosperms as found in *Zea Mays*. As has been observed by many investigators upon chromosome count in endosperm when it consists of many nuclei, the number varies in the different nuclei, there no longer being the $3x$ number. If in some of the divisions, when there is not an equal distribution of chromosomes, which is common in endosperm divisions, one group should pass to one pole and two to the other, the chromatin brought in by the sperm would then be in one nucleus by itself, or with one of the polar nuclei, thus causing the mottled appearance in the endosperm as seen in *Zea Mays*.

The earlier writers on double fertilization, STRASBURGER (**17, 18**), MOTTIER (**14**), NAWASCHIN (**15**), and ERNST (**3**), and the latest investigator SAX (**16**), concluded that there was an intermingling or a complete fusion of the chromatin contributed by the sperm and two polar nuclei in the formation of the primary endosperm nucleus, and ERNST (**3**) further stated that he was unable to recognize at segmentation or in spirem the chromatin that had been contributed by the respective nuclei; but the writer, because of the numerous specimens showing the distinct spirems, the three groups of segments, and the groups on the tripolar spindle, is unable to accept these conclusions for the primary endosperm nucleus of *Trillium grandiflorum* and *Lilium Martagon*.

What has been said for the chromatin of the primary endosperm nucleus of *Lilium Martagon* applies for the most part to that of the fertilized egg of *Trillium grandiflorum* and the early stages of *Lilium Martagon* and *L. philadelphicum*.

After a careful investigation of *L. Martagon* and *L. candidum*, MOTTIER (**13**) reported in 1898 that there is a complete fusion of the male nucleus and the egg nucleus in the resting condition, the chromatin being in a fine network. If the subsequent steps are not followed out, such an interpretation could be made for *Trillium*. Figs. 1 and 2 show fertilized eggs in which the sperm is lying coiled upon the egg, the male chromatin material being in coarser strands than in the egg. In some instances the nuclear membranes separating the nuclei break down early (fig. 3), while in others they persist for some time (fig. 4). It was the appearance of such stages as fig. 3, and some that will be spoken of later, that caused previous investigators (MOTTIER, NAWASCHIN, SAX, STRASBURGER, and others) to conclude that there was a fusion to the extent that the individual components were not recognized.

From sections showing the spirems (figs. 6–11) it appears at first sight that the interpretations of figs. 9 and 10 would be different from those of figs. 6 and 7; for in figs. 9 and 10 two spirems stand out distinctly, while in the other two there appears to be only one. If the reader will consider all the various angles from which the fertilized egg might be cut and all the various positions the two spirems might occupy within the cavity, it will be apparent that frequently the sections might be so cut that the dual nature of the spirems would not be seen. The significance of the contraction, similar to the second contraction of the heterotypic mitosis that occurs just previous to or during segmentation (figs. 11, 12), the writer is unable to interpret. There was no tripolar spindle observed in the fertilized egg, and from the appearance of fig. 13 it seems that only a bipolar spindle is formed and the second group of chromosomes is pulled in upon it. In each group there are approximately six, the haploid number.

In 1891 GUIGNARD (**6**) pointed out in *Lilium Martagon* that there were two spirems and that one-half of the chromosomes on the spindle were contributed by the male parent and one-half by the female parent. No drawings were made to substantiate these views, and ERNST (**3**) and MOTTIER (**13**) apparently made it so conclusive that there was a complete fusion or intermingling of chromatin that GUIGNARD's earlier views were discarded and practically forgotten. In later papers GUIGNARD himself did not place much emphasis upon these earlier views.

SAX (**16**) stated that a spirem was frequently found in the egg and sperm before fusion occurred (fig. 21), but says "the rare appearance of such cases as that of the spirem stage in the egg and male nuclei when their outlines are still distinct, is probably of little significance in this respect. It is probable that these nuclei subsequently fuse completely, because no later stage of incomplete fusion was found."

Many writers have looked upon the number of nucleoli present in the fertilized egg as an indication that fertilization has or has not occurred. This, as ERNST (**3**) has pointed out, is not a safe indicator, for, as shown in figs. 5, 6, 9, 19–23, the nuclei have already united and from two to many nucleoli are present.

SAX (**16**) says "fig. 19 shows a stage where the common boundary has disappeared, the contents apparently mingled, and those from the male and female nuclei are not to be distinguished." In case of the formation of the fertilized egg, as in the formation of the primary endosperm nucleus, the writer is unable to agree with SAX and the earlier writers that there is a complete fusion or intermingling of the chromatin of the egg and the sperm; the material so plainly shows that the two remain separate from the time of coming together until the formation of the daughter nuclei. What happens after that does not come within the scope of this paper.

Conclusions

From the stages that have been found in the fertilized egg leading up to the first division, and in the primary endosperm nucleus up to the time of the third division of the endosperm, it is evident that they are analogous to those of *Pinus*, as reported by FERGUSON (**4, 5**), although nothing was observed that would correspond to those steps in fertilization, as reported by HUTCHINSON (**12**) for *Abies*, which differed from those of *Pinus*.

To the writer the finding of the separate, distinct spirems and the separate groups of chromosomes is added evidence that the chromosomes maintain their individuality from one generation to the next.

In conclusion the writer wishes to state that, according to her interpretation of the word "fusion" as used by previous writers, there was meant a mingling of the male and female chromatin, so that all trace of the individuality of chromatin and chromosomes contributed by the respective parents was lost by the time of the first division. In this investigation no such fusion was found, but instead, an entrance of two or three masses of chromatin, as the case might be, into a more or less single nuclear cavity, the chromatin contributed by the respective parents remaining distinct throughout the preparation for the first division. The writer is unable to state whether fusion in the sense of complete intermingling ever occurs after the completion of the first division.

Summary

1. After the male nucleus and two polar nuclei come together, the separating nuclear membranes persist more or less until segmentation.
2. Three distinct spirems are formed in the primary endosperm nucleus.
3. A tripolar spindle, each arm with its group of chromosomes, precedes the formation of the bipolar spindle.
4. The three groups of chromosomes maintain their identity, at least until several divisions have occurred.
5. The nuclear membranes separating the egg and sperm nuclei disappear earlier than in the preceding case, but the two groups of chromatin remain separate.

6. Two distinct spirems, followed by two groups of chromosomes, arise from the maternal and paternal chromatin in the fertilized egg.

7. There is no complete intermingling of chromatin at fertilization.

To Professor D. M. MOTTIER of Indiana University, under whom the greater part of this work was done, I wish to express my appreciation for the helpful criticisms and help given; to Professor C. B. ATWELL and Professor W. WOODBURN of Northwestern University for the courtesies and encouragement given while working in their laboratory; and to Professor C. J. CHAMBERLAIN of the University of Chicago for the suggestion of this problem.

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EXPLANATION OF PLATES III–V

All figures were drawn with the aid of an Abbe camera lucida, with Bausch & Lomb 1.9 mm. oil immersion, and ocular 6. The magnification of all figures except fig. 29 is ×1500; fig. 29 ×420. The plates are reduced to two-thirds their original size.

PLATE III

FIG. 1.—Early union of egg and sperm in *Lilium Martagon.*

FIG. 2.—A little later stage in *Trillium grandiflorum.*

FIG. 3.—Early prophase, separating membranes between egg and sperm having disappeared.

FIG. 4.—A little later, but separating membranes still present.

FIG. 5.—An interrupted spirem in fertilized egg, spirem being more or less beaded.

FIG. 6.—Early spirem in fertilized egg.

FIGS. 7, 8.—Development of spirem.

FIGS. 9, 10.—Two spirems in each nucleus, line *a–b* separating chromatin contributed by egg and sperm respectively.

FIG. 11.—Contraction at time of segmentation.

FIG 12.—Later, contraction still evident; chromosomes in two groups, nuclear membrane having disappeared.

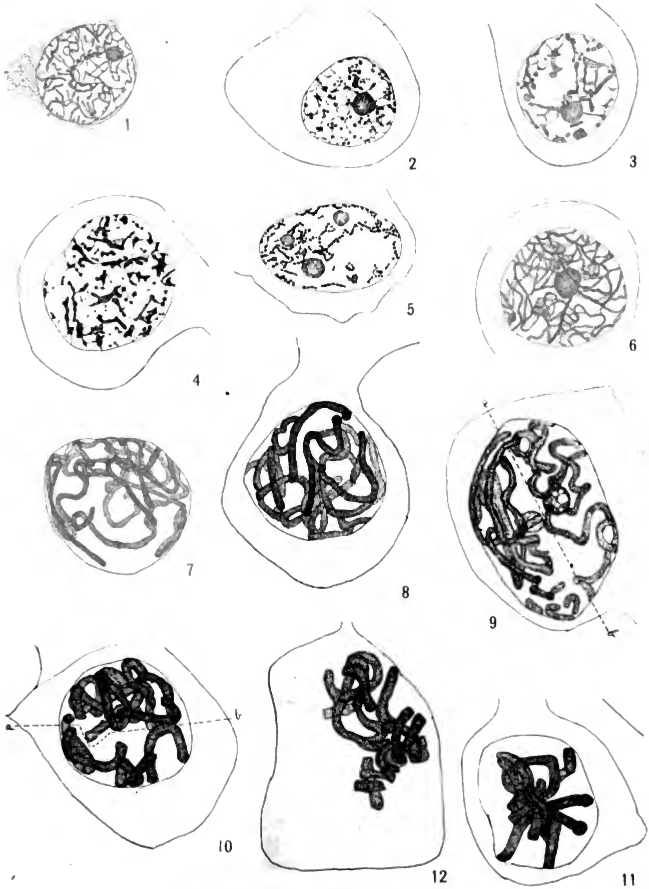
PLATE IV

FIG. 13.—Formation of bipolar spindle, second group being pulled into equatorial plate.

FIG. 14.—Late telophase of first division.

FIG. 15.—Two-celled embryo.

FIG. 16.—*Trillium grandiflorum;* early coming together of three nuclei to form primary endosperm nucleus.



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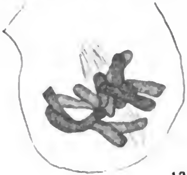
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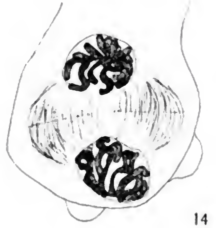
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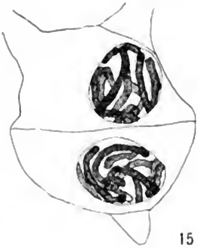
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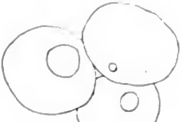
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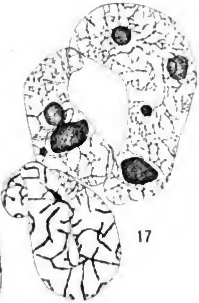
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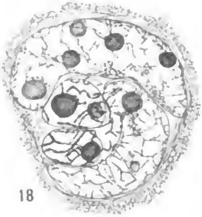
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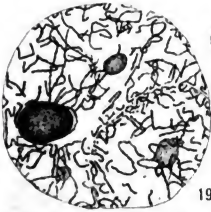
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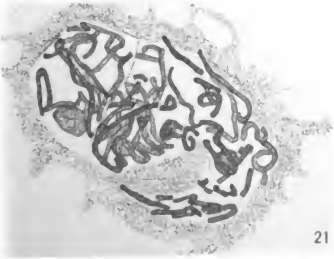
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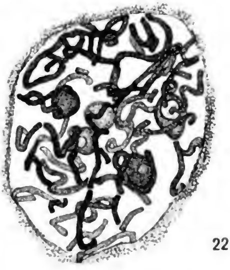
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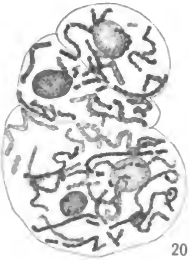

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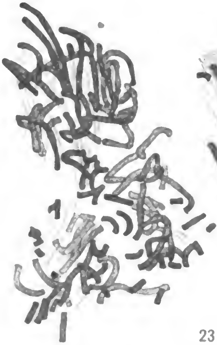

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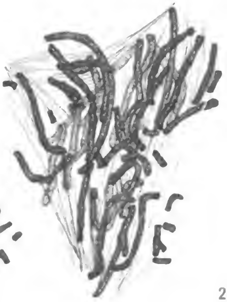

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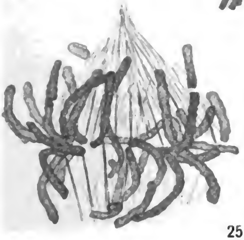

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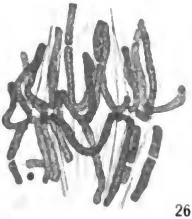

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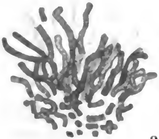

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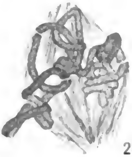

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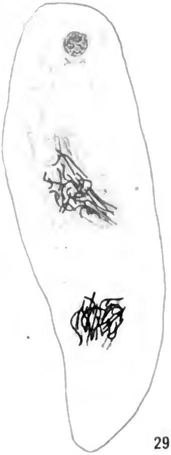

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NOTHNAGEL on FERTILIZATION

FIG. 17.—*Lilium Martagon;* same stage as fig. 16, the three nuclei being curved, sperm being more curved and chromatin coarser.

FIG. 18.—Later; fibers are appearing about nuclear complex.

FIG. 19.—Showing two components of primary endosperm nucleus in which the chromatin is collecting in heavier strands and separating nuclear membranes are still evident.

FIG. 21.—Late spirem; separating nuclear membranes still divide the three spirems; fibers beginning to radiate out into cytoplasm.

FIG. 22.—Next section of same primary endosperm nucleus as seen in fig. 21.

PLATE V

FIG. 20.—Formation of spirem, the three nuclei still separate.

FIG. 23.—Three groups of chromosomes upon a tripolar spindle.

FIG. 24.—Slightly later stage; third group is being pulled in with other two groups to form bipolar spindle.

FIG. 25.—Bipolar spindle of first division of primary endosperm nucleus, third group of chromosomes still separate.

FIG. 26.—Slightly later stage; all individuality of groups of chromosomes lost; chromosomes beginning to split longitudinally.

FIG. 27.—Telophase of first division of primary endosperm nucleus.

FIG. 28.—Third division of endosperm nucleus in *Trillium grandiflorum*, showing 3 groups of chromosomes upon bipolar spindle.

FIG. 29.—Second division of endosperm nucleus, upper one showing three groups of chromosomes.

FACTORS DETERMINING CHARACTER AND DISTRIBUTION OF FOOD RESERVE IN WOODY PLANTS

EDMUND W. SINNOTT

(WITH TWO FIGURES)

Introduction

The investigations of RUSSOW, FISCHER, and others upon the character and seasonal changes of the food reserves in woody plants, and the considerable attention which this problem has more recently received, have made us familiar with many of the important facts which it involves; but as to the underlying causes which determine the type of reserve food occurring in any cell and which direct its changes in form and location we are still uncertain. Our present knowledge, derived in greater part from a study of twigs, branches, and small trunks and roots, may be summarized substantially as follows. The major part of the reserves stored up by trees and shrubs during the productive season is evidently composed of starch (fat is also demonstrable, and SABLON (**5**) has emphasized the importance of reserve cellulose as a center of storage). At about the beginning of winter there is a decided reduction in the amount of starch, leading to its disappearance in the phloem and cortex of practically all woody plants in our latitude. At the same time the amount of fat seems to increase greatly. In certain forms, called by FISCHER (**2**) "starch trees," there is no further change, the food reserves in the pith and wood persisting in the form of starch throughout the winter. In others, called by him "fat trees," the starch vanishes in these portions of the stem as well, and fat appears in abundance, constituting the only visible food reserve during the winter. In all woody plants, late winter or early spring sees a regeneration of starch throughout the tissues of the stem and an apparent diminution in the amount of fat. This regenerated starch is used up in the formation of the spring growth, and it is not until summer that a fresh supply begins to be deposited. It has been supposed that at the seasonal changes starch was converted directly into fat or fat directly into starch, but as microchemical methods have been employed almost entirely this cannot well be proven. The only work involving a quantitative analysis, that of NIKLEWSKI (3), seems to indicate that changes in the two types of reserve food occur independently of each other. It has been observed that the seasonal changes are most marked in twigs and small branches, less so in main stems, and least of all in roots, where fat is scarce and starch persists practically unaltered throughout the winter. The work of FABRICIUS (1) seems to indicate that in the large trunks of spruce conditions may be different from those in small trunks, branches, and twigs, and that starch there may have its maximum in winter and fat its maximum in summer.

That temperature is of importance in producing changes in the character of the food reserves is shown by the fact that starch regeneration may be induced in the winter by bringing twigs from out-of-doors into a warm place. That a subjection to cold during the summer will not cause the characteristic winter changes, however, and that these changes will nevertheless occur in the fall, even though the plants remain under a warm environment, indicate that factors other than temperature must be operative.

The present paper is an attempt to throw light on this general problem by a careful anatomical study of the storage regions of woody plants with a view to determining the exact distribution of starch and fat there and its change from season to season. It contains the results of nearly three years' observations on about 300 species of trees and shrubs belonging to over 100 genera and including all the common species of the northeastern United States, together with many exotic ones in the collections of the Arnold Arboretum. With the exception of a little received from the southern states, all the material studied was gathered in Massachusetts and Connecticut. Special attention was paid to conditions in twigs and young branches, where seasonal changes are most marked. Thin sections of freshly gathered material were cut on the microtome and treated with iodine and Sudan III to bring out the starch and the fat, respectively.

Observations

The results of previous workers as to seasonal changes were substantially confirmed. Although fat is evidently most abundant in the winter months, it is by no means absent during the summer, but at that time it is apt to be masked by the starch. Microchemical evidence as to the relative abundance of either starch or fat at different seasons is necessarily unreliable. It is certain, however, that much of the starch which disappears in the fall does not become converted into fat, but changes to glucose or some other non-visible substance, since in many starch trees large numbers of cells are emptied of starch without causing the appearance of fat. The twigs of some trees, notably species of *Catalpa*, are almost emptied of visible food reserves of all sorts during the winter. There are marked differences between species in their ability to produce fat, as indicated by its abundance in the phloem and cortex. This type of food substance seems to be practically absent in species of *Carya* and is very small in amount in *Fraxinus*, *Acer*. *Syringa*, and others. It is particularly abundant in such forms as *Liriodendron*, *Populus*, and *Pinus*. In general, fat is less abundant in the phloem and cortex of starch trees than of fat trees. There are certain exceptions to this rule, however; notably *Liriodendron*, a starch tree, but rich in cortical fat; and the soft birches, fat trees, but poor in cortical fat. Fat was universally found to be more abundant in the phloem than anywhere else in the plant.

The observations of others that seasonal changes are more marked in twigs than in larger branches and trunks was confirmed. This conservatism is apparently still greater in the roots, where starch was found to be practically unreduced in amount during the winter, a fact recorded by PRESTON and PHILLIPS (4). In the root, too, the amount of fat is very much less than in the stem.

FABRICIUS (1) and others have noted the fact that starch trees are predominantly hard-wooded species and fat trees soft-wooded ones. This rule was in general confirmed by the present study, but a number of exceptions were noticed which we shall later find to be significant. The hard pines, for example, are clearly fat trees; and *Liriodendron*, *Magnolia*, *Ailanthus*, and *Platanus*, all soft-wooded, are clearly starch trees.

Two other general relations between anatomy and the character of the food reserve were noted. Species with diffuse-pored woods are usually either fat trees or have an abundance of fat; those with ring porous wood are almost always starch trees. Narrow-rayed species may belong to either category, but broad-rayed types are prevailingly starch trees.

By no means all the species studied could be classed definitely as starch trees or fat trees. The oaks, ashes, and hickories belong clearly to the former category, and the pines and lindens to the latter; but very many species are intermediate in character, possessing both fat and starch in the wood of the stem. In many instances, also, storage material was noted which was neither starch nor fat but seemed somewhat intermediate in character between the two. The outlines of the original starch grains could sometimes roughly be made out, but the starch content of the cell was apparently coalescing into an irregular brownish mass. This was insoluble in ether and stained neither with iodine nor Sudan III. Its bulky, opaque character indicated that it was actually storage material and not merely the cytoplasm of the cell. It was evident chiefly during the winter, occurring frequently in the cortex as well as in the wood, in cells which had been filled with starch. SUROZ (**6**) called attention to the existence of such material, but apparently it has not been noted by others. If it is indeed a stage in the transition from starch to fat, its composition might perhaps throw light on the difficult problem of the chemistry of fat production in the cell.

Table I presents a rough outline of the character of the food reserve in the pith and wood of the stem (twigs and young branches) of the more common trees and shrubs during the midwinter months, dividing them into those where fat predominates, those which possess considerable amounts of both starch and fat, and those in which starch predominates. This classification should not be regarded as rigid, since a considerable variation has been noted in some of the species and genera, but it represents the average condition observed for each. The character of the reserve in phloem and cortex of course is not included in this table.

The most noteworthy facts brought out by these anatomical investigations, however, concern the exact distribution of the reserve foods in the tissues and their changes from season to season. In all species starch disappears in the fall almost completely from phloem and cortex, and even in the starch trees it is much reduced in the wood as well. The reduction in the wood takes place first and most extensively in the regions *immediately around the vessels.* In many

TABLE I

TYPE OF FOOD RESERVE IN PITH AND WOOD OF STEM (TWIGS AND YOUNG BRANCHES) OF VARIOUS WOODY PLANTS DURING MIDWINTER

PREDOMINANTLY FAT	BOTH STARCH AND FAT
Aesculus	Abies
Betula (some species)	Alnus
Catalpa	Betula (some species)
Cornus (some species)	Chamaecyparis
Dirca	Ginkgo
Juglans (some species)	Gordonia
Leitneria	Juglans (some species)
Picea	Populus (some species)
Pinus	Prunus
Populus (most species)	Rhus (most species)
Pseudotsuga	Robinia
Rhus (some species)	Salix
Taxus	Sambucus
Tilia	Viburnum (some species)
Tsuga	
Viburnum (some species)	

PREDOMINANTLY STARCH

Acer
Ailanthus
Berberis
Carpinus
Carya
Castanea
Celtis
Cephalanthus
Cladrastis
Cornus (some species)
Crataegus
Deutzia
Diervilla
Diospyros
Elaeagnus
Evonymus
Fagus
Fraxinus
Gleditsia
Hamamelis
Hydrangea
Ilex
Itea
Jamesia
Kalmia
Lindera
Liquidambar
Liriodendron
Lonicera
Magnolia
Nyssa
Philadelphus
Platanus
Quercus
Rhamnus
Ribes
Rosa
Sassafras
Styrax
Symphoricarpos
Syringa
Ulmus
Vitis
Xanthoxylum

species starch is poorly developed here even in summer. It is in these regions, too, that the "transitional" material is very apt to appear. Furthermore, even in typical starch trees the wood parenchyma cells or ray cells which directly adjoin a vessel frequently contain fat; and in species where both starch and fat occur in the wood the fat is conspicuously abundant near the vessels. In the medullary rays of such forms as most of the poplars and willows, for example, fat is found chiefly in those ray cells which touch a vessel and starch in those which adjoin nothing but fibers. This tendency for starch to be absent and fat to be present in the immediate vicinity of the vessels is obvious in all woody plants in the midwinter season, and suggests that the character of the food reserve may be related in some way to the water supply.

Another anatomical feature which is clearly associated with the kind of food stored in a cell is the character of the cell wall. Wherever this is strongly lignified, thick, and provided with few and small pits, starch tends to remain unchanged throughout the winter. When it is thin or provided with many and large pits, starch tends to disappear and fat to be abundant. Thus in the storage cells of phloem and cortex, the walls of which are quite unlignified, starch vanishes early and completely and fat is very common. In the heavily lignified, thick-walled pith cells which occur in so many species starch remains throughout the winter, and in such cells the reserve food is less modified than in almost any other part of the stem. In branch gaps, where such a pith meets the cortex, the line between the starch-containing and the fat-containing cells is absolutely sharp and coincides exactly with the line between the lignified and the unlignified tissue.

A study of the vertical and ray parenchyma of the wood, the chief seats of food storage in the xylem itself, is particularly instructive in this connection, and furnishes us with a definite anatomical distinction between starch trees and fat trees. Where these cells are thick-walled and have few and small pits, starch predominates; where the walls are thin and well pitted, fat predominates. In hard-wooded species (fig. 1), long noted as starch trees, the parenchyma shares certain of the characters of the other wood cells and has thick, well lignified, square-cornered, and small-pitted walls.

In soft-wooded species (fig. 2), on the other hand, well known as being prevailingly fat trees, the vertical and ray parenchyma is thinner-walled and less heavily lignified, and the cells of the rays tend consequently to be irregular in shape, with oblique or bulging end walls, an outline quite different from the prevailingly rigid and rectangular one of starch tree parenchyma. They are well provided with pits or are so thin as not to require pitting.

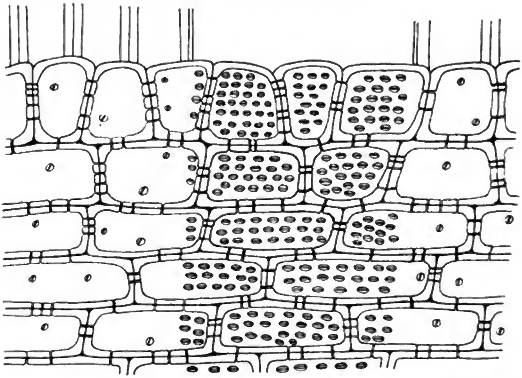

Fig. 1.—*Nyssa sylvatica*, a starch tree: portion of medullary ray of wood seen in radial section as it crosses fibers (at left and right) and a vessel (in center); note thick-walled, squarish ray cells; small pits between ray cells and from ray cells to fibers; and large pits from ray cells to vessel.

Of particular significance are the exceptions already noted to the general rule that there is a connection between hardness of wood and type of food reserve. The hard-wooded pines, for instance, are filled with fat, a circumstance evidently related to the fact that their ray parenchyma and resin canal epithelium (the only seats of storage in the wood) are unlignified and very thin-walled. In *Liriodendron*, *Magnolia*, *Ailanthus*, and *Platanus*, on the other hand, which are soft-wooded but which we have nevertheless observed to contain starch, the rays are made up of thick-walled rectangular cells precisely like those of starch trees. This type of ray cell is here evidently mechanical in its function, since all these species have wide rays which might collapse or be badly crushed were they not built of strong-walled cells. The vertical parenchyma of these soft-wooded starch trees tends to have thinner walls, and in *Liriodendron*, at least, it contains considerable fat.

On the basis of these facts we are forced to conclude that the hardness of a wood affects the type of food reserve indirectly, through its influence on the walls of the storage cells. In certain cases, however, this effect is evidently more direct. The hard-wooded species of *Cornus*, such as *C. florida*, are starch trees, and the soft-wooded ones, such as *C. stolonifera*, are fat trees, although there is no very striking anatomical difference between the parenchyma cells of the two groups. The same fact is noticeable in the hard- and soft-wooded species of *Viburnum* and birches. In these cases it is fair to assume that the high or low degree of lignification

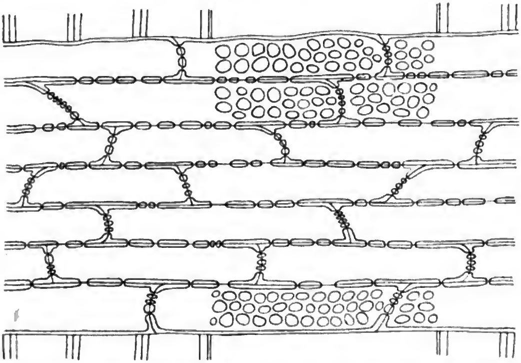

FIG. 2.—*Populus grandidentata*, a fat tree: medullary ray of wood seen in radial section as it crosses fibers (at left and right) and a vessel (in center); note thin-walled ray cells, with slanting or rounded ends, and large pits from ray cell to ray cell and from vessel to (marginal) ray cells.

of the conducting and fibrous cells is shared by the parenchyma, and that it is the actual hardness of the wall rather than its structure and pitting which is related to the character of the stored food. We shall later suggest a cause for this relation.

Conditions in starch fibers are of interest here. These are fiber-like, starch-containing cells, and are frequently found in the maples, willows, certain legumes, and other trees. Unlike the parenchyma cells, which are definitely connected with the water supply either by their position next to a vessel or tracheid, or by being linked therewith by other parenchyma cells, these starch fibers usually occur in the midst of non-conducting tissue, being surrounded by fibers of the ordinary type. They possess very small, frequently rudimentary, pits and usually are thick-walled. No instance has been observed by the writer where any reserve food but starch occurs in such cells, and this starch usually stains much more deeply with iodine than that of the ordinary parenchyma, indicating that its water content is lower. The persistent character of the food reserve in these starch fibers is evidently related both to their isolation from channels of water conduction and to their thick and pitless walls.

Discussion

These two main facts which our anatomical survey brings out, (1) that during the winter starch is commonest in regions remote from centers of conduction (both in xylem and phloem), and in cells with thick, well lignified, and small-pitted walls, and (2) that fat is most abundant close to vessels or tracheids, in the phloem, and in cells with thin or unlignified walls and large pits, at once suggest that *the character of the food reserve depends primarily upon the ease with which water or substances carried in water have access to the storage cells.* Where access is slow and difficult, the reserve remains in its summer condition as starch. Where access is easy, it is converted to a greater or less degree into other substances, with the consequent appearance of fat.

In storage cells the walls of which are unlignified, as in the phloem and cortex of all species, and the rays and canal epithelium of *Pinus*, starch is quite absent in the winter and fat is very abundant. There is evidently no impediment to thorough diffusion in such tissues, and conversion may take place far from any center of water conduction.

Where the wall of the storage cell has become heavily lignified, however, even though it is provided with pits (which in such cases are usually very small), diffusion seems to be much impeded, and the reserve food remains unchanged throughout the winter. This is well shown by the terminal cell in the medullary ray of a typical starch tree, which cell, filled with starch and surrounded by its lignified wall, abuts directly upon a starchless, fat-filled cell of the cambial region. There are small pits in the wall between these two cells, but the wall nevertheless seems to serve as an effective barrier between them in preventing rapid diffusion. The same circumstance may often be noted where a ray cell touches a vessel. Here the wall between the two is provided with many large pits (fig. 1), so that communication must be easy. The ray cell in this case is usually without starch in the winter and generally contains some fat. Its neighbors at either end, however, are often full of starch but contain no fat. The tangential ray cell walls, although provided with small pits, seem here also to be permeable with difficulty. This leads us to believe that heavy lignification of the wall is a decided hindrance to the ease of diffusion between cells, and that the pits in such a case are for some reason, perhaps because of their very small size, unable to perform their normal functions.

If the wall of the storage cell is less heavily lignified, or is thinner or more abundantly pitted, entrance of water is evidently easier, and we have noted that in these cases starch is more completely converted and fat is more common. In some instances fat may be limited to the cells directly adjacent to a vessel. In others it may extend to adjoining cells, starch occurring only in the more isolated regions. In these cases fat may be observed extending in from the cambial region along the rays for a considerable distance, thus indicating that diffusion takes place between the cells of the phloem region and the ray cells and affording a marked contrast to conditions at the ends of the rays in starch trees. In the true fat trees diffusion is evidently still more easy, for fat occurs throughout the rays and parenchyma, even in regions remote from centers of conduction.

In the cases of *Cornus*, *Viburnum*, and others which we have noted, where the degree of lignification of the walls of the storage cells seems to be a factor which determines the character of the food reserve, it probably operates by rendering easy or difficult the diffusion of water into the cell.

That the starch in starch fibers is never converted into fat is evidently due to the fact that there can be little or no communication between them and the water-conducting elements. The willows are illuminating in this connection. Here the phloem, cortex, and medullary rays contain abundant fat in the winter and very little starch, so that the willows have often been regarded as fat trees. In the last annual ring, however, there frequently occur large numbers of starch-filled fibers, so that some writers have included the willows among starch trees. These fibers are almost absolutely pitless. Diffusion of water among them must thus be a slow process, a fact which probably explains this persistence of starch here where it is lost elsewhere in the wood.

This hypothesis, that the character of the food reserve in a cell is dependent primarily upon the ease with which water or substances carried by water can pass from cell to cell, thus makes more understandable the various facts which have been observed as to the type and distribution of reserves in the stems of woody plants from season to season, and is the contribution of anatomy to the problem under discussion. With this as a basis we may allow ourselves to speculate a little as to just what factors are operative in causing the seasonal changes in the food reserve. That change of temperature alone is quite insufficient to account for these is shown by the fact that they take place in plants kept over winter in the greenhouse. The writer has also observed their occurrence in trees growing in the frostless area of the Gulf states. The changes are doubtless due in the last analysis to the action of enzymes, presumably diastase and lipase. There are evidently two quite distinct series of processes, those concerned with changes in starch, and involving the action of diastase, and those concerned with changes in fats, involving the action of lipase.

Two ways at once suggest themselves through which ease or difficulty of diffusion might affect this enzyme activity. First, the water content of the cells may be modified, those to which water has easy access having a higher content than those which are more isolated or protected. That such a condition actually occurs is indicated by the fact that the starch grains in cells near vessels usually stain more lightly with iodine than the others, showing that they possess a higher proportion of water. Differences in water content doubtless affect the whole physiological activity of the cell and may well determine the type of enzyme action. As to why, on this supposition, there should be such radical seasonal alterations, however, is not clear. There are doubtless changes in the water content of the tissues after leaf-fall and again at the spring awakening, and these changes will of course be felt most by those cells to and from which diffusion is easy. In the case of fat, at least, we know that abundance of water favors lipolytic action, and paucity of water favors the synthesis of fat, facts which probably help to determine the increase or decrease of fat with the seasons.

A second suggestion is that the enzymes themselves are carried by the water as it diffuses through the tissues, and thus effect the characteristic changes in the cells which they enter. That these changes take place in the fall we may perhaps ascribe to the presence of enzymes in the sap which is withdrawn into the tissues of the stem from the leaves before the latter are shed. The enzymes would thus be particularly abundant in the phloem, the ordinary channel of conduction from the leaves downward, and they probably would occur in the water of the vessels. They would be progressively less common in those parts of the plant farthest from the leaves. This would explain (1) why the changes are most marked in the phloem and adjacent regions and around the vessels; (2) why they are more marked in twigs than in branches and trunks; and (3) why in roots they are practically absent.

To determine whether or not lipase is actually present in leaves, a series of experiments was undertaken. The leaves of a number of species of trees were gathered in the latter part of summer, dried, and finely pulverized, and the leaf powder of each was mixed with olive oil and bottled up, a number of bottles being made for each species. The proportion by weight of powder and oil was the same in every case. These were kept at room temperature, and once a week a bottle of each species was taken, the oil was removed from the powder by filtration and was titrated against N/10 sodium hydroxide. The rate of increase of acid measured the strength of the lipolytic action and hence, probably, the amount of lipase. Results showed the ferment to be most abundant in the leaves of those species in which fat was commonest in the stems in winter.

To determine the exact method by which these seasonal changes in the food reserve are effected, however, is beyond the scope of the present paper, the purpose of which is to emphasize the important part evidently played by the minute anatomy of the stem and root in determining the ease of diffusion of water or solutions throughout their tissues and thus affecting the character, distribution, and seasonal alterations in the stored foods, and doubtless in other functional activities of the plant. We may point out that in any such physiological problem as this one a thorough knowledge of the structures concerned is absolutely essential before sound conclusions can be reached.

Summary

1. Previous observations upon the character, distribution, and seasonal changes of the food reserves of woody plants in temperate regions were in general confirmed by the present investigation and were considerably extended.

2. A study of the minute distribution of the food reserves in the tissues of the stem (twigs and young branches) during the winter shows that (1) starch is commonest in regions remote from centers of conduction and in cells with thick, well lignified, small-pitted walls; and (2) fat is most abundant in and near the phloem, close to vessels, and in cells with thin or unlignified walls or large pits.

3. These facts indicate that the character of the food reserve in any cell depends primarily upon the ease with which water or substances carried by water have access to the cell. Where the movement of liquids is apparently slow and difficult, the reserve persists as starch; where such movement is easy, starch disappears at the beginning of winter and fat is produced.

4. This suggests that differences in the type of food reserve may be due to (1) differences in water content of the various storage cells, resulting in modification of enzyme activity, or (2) differences in the ease with which enzymes have effective access to the storage cells.

The writer wishes to thank the authorities of the Agricultural Experiment Stations of Louisiana and of Florida for material from their states, and the authorities of the Arnold Arboretum for specimens from their extensive collections of trees and shrubs. For several helpful suggestions he is also indebted to Professor W. J. V. OSTERHOUT of Harvard University.

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BRIEFER ARTICLES

MODIFIED SAFETY-RAZOR BLADE HOLDER FOR TEMPERATURE CONTROL

(WITH ONE FIGURE)

The apparatus devised in this laboratory for cutting frozen plant material on the rotary microtome[1] has been found useful in the cutting of paraffin sections also, especially when a modification of the familiar safety-razor blade holder is employed. For the control of the temperature of the knife in cutting paraffin sections LAND[2] describes and figures a trough of metal provided with a nipple at either end in which the microtome knife is placed and through which water of the desired temperature is made to flow. The use of a Gillette safety-razor blade in a proper holder is apparently becoming rather general among plant cytologists. Certainly the use of such blades with classes in microtechnique is a great saving of time and energy as compared with attempts either to allow the students to sharpen microtome knives themselves or to provide them with such knives properly sharpened. In addition, with such a class, consistently successful results in cutting can only be obtained if it is possible to regulate the temperature of the knife and, in some cases, of the material also. Even at 10 μ with refractory material in 52° paraffin it is difficult for most students always to obtain a smooth ribbon at ordinary laboratory temperatures unless the knife is kept cool. To meet this latter situation a simple modification of the usual type of safety-razor blade holder has been employed with such success in this laboratory that a brief description of it seems desirable. We have found the original holder made by STRICKLER[3] the most desirable type of a number at present on the market. To such a holder a small brass tube is attached, as shown in fig. 1. This tube has a bore of 4 mm. and is soldered to the outer leaf of the holder, thus in no way interfering with the separation of the leaves when the safety-razor blade is to be inserted. The tube is extended approximately 6 mm. beyond the holder proper at either end to allow the attaching of small rubber tubes.

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[1] GARDNER, N. L., A freezing device for the rotary microtome. BOT. GAZ. **63**: 236–238. 1917.

[2] LAND, W. J. G., A method of controlling the temperature of the paraffin block and microtome knife. BOT. GAZ. **57**:520–523. 1914.

[3] CHAMBERLAIN, C. J., Methods in plant histology. Chicago. 1915 (p. 9).

For class use, where very thin sections are not ordinarily required, we have found that the temperature of the knife in such a holder is sufficiently low if tap water is allowed to flow through the tube. A very short time is required for the temperature of the water to be communicated to the knife. A cooling cell such as LAND's or GARDNER's also regulated with tap water may be employed in addition, but its use in most cases is superfluous. Where sections from soft or medium paraffin under 5 μ are required, the modified safety-razor blade holder and the cooling cell are attached to GARDNER's apparatus with the buckets filled with ice water. Under such conditions sections 2 μ thick have been cut very successfully from a paraffin melting at 53°.—T. H. GOODSPEED, *University of California.*

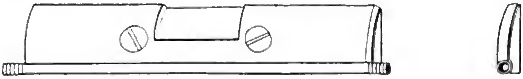

FIG. 1

POLLINATION OF ASCLEPIAS CRYPTOCERAS

Being interested in the mode of pollination of *Asclepias*, I should like to know how PAYSON explains the mode of pollination given in BOT. GAZ. **61**:73. 1916. By a bumblebee's foot I understand the end of the last tarsal joint with two claws and a pulvillus. Does the corpusculum become attached to the foot or to one of these appendages? If the foot is wedged between the anther wings, how does the bee get away without tearing the anther wings, and how does it, or any part of it, enter the cleft of the corpusculum? In pollination, if the bee pulls out its foot with attached corpusculum, what keeps the pollinium from coming out with it? My view of the pollination of *Asclepias*, published in BOT. GAZ. **11**:262–269. 1886, and **20**:110. 1895, is that a single claw, hair, pulvillus, tibial spur, or stump of a retinaculum is caught in the slit between the anther wings and is guided by them into the cleft of the corpusculum. The corpusculum keeps this appendage from again entering the slit. Only one pollinium is caught between the wings and guided into the stigmatic chamber, where it is held so firmly that a pull breaks it loose from the retinaculum. Probably *Asclepias cryptoceras* is a bumblebee flower, but I would not accept the view that it is not occasionally pollinated by other long-tongued bees, or butterflies, unless it is shown that these insects do not have proboscides long enough to reach the nectar.—CHARLES ROBERTSON, *Carlinville, Ill.*

CURRENT LITERATURE

NOTES FOR STUDENTS

Estimation of plant carbohydrates.—In a series of papers from the Rothamstead Experimental Station, DAVIS, DAISH, and SAWYER have reported the results of a critical study of existing methods for the estimation of carbohydrates in plant extracts, and have suggested a number of improvements and modifications designed to secure greater accuracy. In the initial paper of the series, on the estimation of maltose in solution with other sugars, DAVIS and DAISH[1] point out several sources of possible error in the gravimetric method of BROWN, MORRIS, and MILLAR. All samples of asbestos examined, even after previous washing in acid and ignition, contained an easily decomposed silicate, which was rapidly dissolved by the hot alkaline Fehling's solution, thus giving weights which were uniformly too low. Digesting the asbestos for 30 minutes with boiling 20 per cent NaOH and subsequent washing with water removes all material soluble in Fehling's solution, and the authors recommend such digestion as a routine procedure. Since the precipitate of cuprous oxide obtained from plant extracts or from solutions previously subjected to fermentation by yeasts invariably contains copper salts of amino acids and adsorbed colloidal organic matter, the employment of the official method of weighing cuprous oxide as such after drying at 100° introduces an error. This is partially corrected by placing the crucible, after previous washing with alcohol and ether and drying at 100° in a larger crucible and heating for 30 minutes, without the use of a blowpipe, in a powerful flame, subsequently weighing as cupric oxide.

Of the more generally employed volumetric methods subjected to test, the Ling-Rendle method, employing an acid solution of ferrous ammonium sulphate and ammonium thiocyanate as indicator for Fehling's solution, is accurate to at least 0.3 per cent, and is also much more rapid than the Bertrand permanganate method. The latter was found to have an error of 1 per cent with maltose, 1.5 per cent with dextrose, while the results for cane sugar were 3.5 per cent low, as the 2 per cent HCl used for inversion caused considerable decomposition of levulose. In estimating cane sugar in solutions containing maltose, it is impossible to use HCl at 70° for inversion, since maltose is also hydrolyzed, while pentoses undergo decomposition; nor can 2 per cent citric acid be employed, since the use of basic lead acetate to precipitate tannins, amino acids, etc., and the subsequent precipitation of lead with Na_2CO_3, leaves in solution a quantity of sodium acetate sufficient to practically inhibit inversion by 2 per cent acid. The authors find that 10 minutes' boiling with 10 per cent citric acid completely hydrolyzes cane sugar without affecting maltose or decomposing pentoses, and recommend this method. Inversion by invertase also gave quantitative results which were too low, apparently, because maltose is carried down in the precipitation with alumina cream. It was impossible to estimate maltose in plant extracts by hydrolysis for 3 hours with dilute boiling HCl or H_2SO_4, as recommended by BROWN and MORRIS, since there was destruction of at least 30 per cent of the levulose present, with measurable amounts of dextrose, by such treatment with any concentration of acid sufficient to effect complete hydrolysis of the maltose present. Hydrolysis with 2.44 per cent HCl at 70° gave no better results; in a 1 per cent solution only 94 per cent of the maltose had been converted after 24 hours' boiling and there had been material destruction of the levulose present. The authors therefore adopted fermentation of the maltose-containing solution with pure cultures of maltose-free yeast as the only satisfactory procedure. The solution is freed of tannins, amino acids, etc., with basic lead acetate, is then made lead-free by adding solid Na_2CO_3, filtering, acidifying, treating with H_2S, and finally making slightly acid to litmus with dilute Na_2CO_3. Three yeasts, *Saccharomyces exiguus*, *S. anomalus*, and *S. marxianus*, were used, the fermentation being continued at 25° for 31 days. All gave good results, but *S. exiguus* is best for general use, since it is least sensitive to acid and its less bulky growth causes less contamination of the cuprous oxide precipitate with salts of amino acids. Checks fermented with ordinary distillery yeasts permit the making of a correction for pentoses remaining after the other sugars have been destroyed. Pentoses were determined by distillation of an aliquot of the solution with HCl at 70° and weighing the furfural as phloroglucide.

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[1] DAVIS, WILLIAM A., and DAISH, ARTHUR JOHN, A study of the methods of estimation of carbohydrates, especially in plant extracts. I. A new method for the estimation of maltose in presence of other sugars. Jour. Agric. Sci. 5:437–468. 1913.

The authors' assertion that maltose is hydrolyzed by HCl at 70° has been questioned by KLUYVER,[2] and DAVIS has consequently presented further evidence[3] by reporting the results of a series of experiments with a 1 per cent solution of maltose, carried out under exact Herzfeld conditions, which show a rather uniform loss by hydrolysis of about 2 per cent of the maltose present.

The authors present a scheme for the analysis of plant extracts which may be summarized as follows. The extract is evaporated to small volume in vacuo and made up to 500 cc. Duplicate 20 cc. portions are evaporated to dryness and the drying completed in vacuo for dry matter determinations. The remainder of the solution is treated with basic lead acetate, filtered, and made up to 2000 cc. A portion of this is freed of lead, made up to convenient volume, and divided into two portions. Upon one of these a determination of direct reduction, representing total dextrose, levulose, maltose, and pentoses, is made; the other is employed for determination of cane sugar by inversion with 10 per cent citric acid and with invertase. The remainder of the 2000 cc. of solution is freed of lead and divided into portions. Upon one of these maltose is determined by fermentation with *S. exiguus* or other maltase-free yeast, checked by fermentation with ordinary yeast; the remaining portion is distilled with HCl for the determination of pentoses.

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[2] KLUYVER, A. J., Biochemische Suikerbepalingen. pp. 223. Boekhandlung E. J. Brill, Leiden. 1914.

[3] DAVIS, WILLIAM A., The hydrolysis of maltose by hydrochloric acid under the Herzfeld conditions of inversion. A reply to A. J. KLUYVER. Jour. Agric. Sci. **6**:413–416. 1914.

The second paper of the series deals with the methods of estimating starch in plant material.[4] The modified Sachsse method, in which starch is hydrolyzed by boiling HCl, is said to be valueless for two reasons: such plant materials as leaves and seeds contain pentosans and other compounds which are broken down, yielding reducing sugars which are computed as dextrose, while the prolonged boiling with acid destroys some of the dextrose present. O'SULLIVAN's method of estimating starch by converting it into a mixture of dextrin and maltose by the use of ordinary diastase is also shown to give rise to low results; plant material freed of sugar by alcohol extraction still contains tannins, amino acids, and other compounds which necessitate precipitation with basic lead acetate, and a considerable quantity of the dextrin present (15–20 per cent under the conditions of the experiments) is carried down by the lead precipitate and thus lost to the analysis. The authors show that this loss of dextrin is avoided by the use of taka-diastase. When taka-diastase is allowed to act for 6 hours at 38° upon previously gelatinized starch, the whole of the starch is converted into a mixture of maltose and dextrose, continued action resulting in a steady increase in the amount of dextrose, until final equilibrium is attained. The authors therefore adopt the following method. Material for analysis is prepared by dropping the freshly collected leaves or other parts into boiling 95 per cent alcohol to which 1 per cent of concentrated ammonia has been added; immediate destruction of all enzymes is thus assured. Sugars are removed by 18–24 hours' continuous extraction in a special apparatus of the Soxhlet type; the material is freed of alcohol by pressing in a Buchner press and drying 18 hours in a steam oven. It is then ground and bottled for analysis. Samples taken for analysis are dried in vacuo before beginning actual work upon them. As leaf materials usually contain considerable quantities of gum, amylans, and other non-starch constituents which yield reducing sugars, it is necessary to remove these by extraction with a large volume of water for 24 hours at 38°, followed by thorough washing. The material is now boiled with water 30 minutes to gelatinize the starch, cooled to 38°, taka-diastase added (0.1 gm. for 10 gms. vacuum-dried material), and the mixture kept for 24 hours at 38° after the addition of a little toluene. The diastase is then destroyed by boiling, the residuum is filtered, washed, the solution made to volume, precipitated with lead, using care to avoid an excess, and portions are taken for polarization and for reduction. Values for the maltose-dextrose mixture are then calculated from the tables of BROWN, MORRIS, and MILLAR.

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[4] DAVIS, WILLIAM A., and DAISH, ARTHUR JOHN, Methods of estimating carbohydrates. II. The estimation of starch in plant material. The use of taka-diastase. Jour. Agric. Sci. 6:152–168. 1914.

DAISH[5] has determined the cupric reducing power of xylose and arabinose under the standard conditions prescribed by BROWN, MORRIS, and MILLAR, as all previously published values were determined under somewhat different conditions. He presents tables of the reducing power of each of these sugars for quantities between 10 and 200 mgm. Two curves obtained by plotting the reducing power, expressed as CuO, against the weight of sugar employed are given; from these curves it is possible to determine the weight of sugar corresponding to any given weight of CuO by the employment of a divisor number. The reducing powers of xylose and arabinose are almost identical and differ very little from that of dextrose; thus for 100 mgm. of sugar the divisor number for dextrose is 2.358, for arabinose 2.536, and for xylose 2.490.

DAVIS and SAWYER[6] have presented evidence that free pentoses are quite generally present in the alcoholic extracts of plant material. This evidence they summarize; there are present substances which are soluble in 80 per cent alcohol, which are not precipitable by basic lead acetate, which are not fermentable by ordinary yeasts, and which give the solution reducing power after all fermentable sugars have been destroyed by yeast. This reducing power, if calculated as that of a mixture of xylose and arabinose, agrees almost exactly with the pentose value of the phloroglucide obtained by a KRÖBER-TOLLENS distillation of the solution after previous precipitation with basic lead acetate. These facts can only be explained upon the assumption that the furfural obtained in distillation is derived from free pentoses, not from pentosans, gums, or other sugars.

Various plants, as marigold, turnip, carrot, potato, *Helianthus*, and *Tropaeolum*, showed the presence in the leaves of pentoses in amounts ranging from 0.3 to 1.0 per cent of the total vacuum-dried material, when determinations were made by the KRÖBER-TOLLENS method upon material prepared according to the authors' method. The presence of other sugars, as cane sugar, in the solution to be distilled gives results which are considerably above the true pentose content. Consequently it is necessary, when very accurate determinations of pentoses are desired, to remove the other sugars by fermenting with *Saccharomyces cerevisiae* and to make the determination by distillation of the fermented solution.

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[5] DAISH, ARTHUR JOHN, Methods of estimation of carbohydrates. III. The cupric reducing power of the pentoses xylose and arabinose. Jour. Agric. Sci. **6**: 255–262. 1914.

[6] DAVIS, WILLIAM A., and SAWYER, GEORGE CONWORTH, The estimation of carbohydrates. IV. The presence of free pentoses in plant extracts and the influence of other sugars on their estimation. Jour. Agric. Sci. **6**:406–412. 1914.

The most recent paper of the series[7] reports the results of an investigation of the generally accepted idea that an excess of basic lead acetate, when added to a solution of invert sugar, precipitates a portion or all of the levulose present as a soluble lead salt. This idea is shown to be incorrect; levulose in dilute solutions is not precipitated by basic lead acetate, even in the presence of chlorides, sulphates, or carbonates. If the acetate be added in excess and allowed to act upon the sugars for a considerable length of time, the amount of levulose present decreases progressively with increase in the time during which the lead is allowed to act. This is due to the formation from the levulose, not of a lead salt, but of a substance having a lower reducing power and much less optical activity than has levulose. It is suggested that this substance may be glutose, which was made by LOBRY DE BRUYN and VAN EKENSTEIN by heating a 20 per cent levulose solution with lead hydroxide at 70-100°, and which was described by them as having about one-half the reducing power of dextrose and as possessing only very slight optical activity. DAVIS considers that basic lead acetate acts at ordinary temperatures in the same way as does lead hydroxide, the action becoming more rapid as the temperature rises.

In order to avoid any loss of levulose when clearing a solution, the basic lead acetate must be added little by little in the cold until precipitation of the impurities is just complete, care being taken that the excess employed is not greater than 1 cc. per 100 cc. of sugar solution (best accomplished by making preliminary tests upon small portions of the filtrate). The solution should at once be filtered through a Buchner funnel, washed, and the excess of lead immediately precipitated by the use of Na_2CO_3 or Na_2SO_4. If excess of Na_2CO_3 be avoided and the solution be shaken up with a little toluene, it may be kept for months without the occurrence of any change. This treatment is very much to be preferred to the use of normal lead acetate, which fails to wholly remove optically active gums and which is a poor clarifying agent, but it is essential to accuracy that the precipitation be conducted in the cold.

The papers here reviewed were preliminary to a series on the formation and translocation of carbohydrates in plants, to be reviewed later.—JOSEPH S. CALDWELL.

Taxonomic notes.—ARTHUR,[8] in continuation of his studies of the Uredineae, has described 23 new North American species in the following genera: *Uromyces* (2), *Puccinia* (8), *Aecidium* (10), *Uredo* (3). The majority of them are from Mexico and Central America.

ASHE[9] has described a new *Vaccinium* (*V. Margarettae*) from the mountains of Georgia and South Carolina, where it occurs in association with *V. vacillans*.

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[7] DAVIS, WILLIAM A., The estimation of carbohydrates. V. The supposed precipitation of reducing sugars by basic lead acetate. Jour. Agric. Sci. **8**:7-15. 1916.

[8] ARTHUR, J. C., New species of Uredineae. X. Bull. Torr. Bot. Club **45**:141-156. 1918.

[9] ASHE, W. W., Notes on southern woody plants. Torreya **18**:71-74. 1918.

EVANS[10] has described 4 new species of *Lejeunea* from Florida, 2 of which seem to be endemic to that state. Of this group of liverworts Florida is now known to contain 44 species of the 48 recorded from the United States.

FERNALD[11] has described 2 new species of *Rosa* (*R. johannensis* and *R. Williamsii*) from northern Maine and adjacent Canada.

PETCH[12] has described 138 new species of fungi from Ceylon, representing approximately 75 genera. Among them there are 32 new species of *Uredo*.

WIEGAND[13] has published the result of his studies of *Elymus* in Eastern North America, discussing 7 species, one of which (*E. riparius*) is described as new.—J. M. C.

Phylogeny of Filicales.—In continuation of his studies of Filicales, BOWER[14] has presented the Pteroideae. The observed details of phyletic relationships among the genera are too numerous to recite, but the paper contains a wealth of material for the special student. In a former paper of the series BOWER suggested that the leptosporangiate ferns, exclusive of the Osmundaceae, may be grouped into two phyletically distinct series: the Superficiales, in which the origin of the sorus is constantly from the surface of the leaf; and the Marginales, in which it is as constantly from the margin. All of the Pteroideae belong to the Marginales, and they show analogies with the Superficiales, especially in those forms which have apparently superficial sori. He shows that such sori result from "a slide of the marginal sorus to a superficial position." "The Superficiales are believed to represent ferns in which that slide took place so early in their descent that the two sequences must be held to be phyletically distinct, notwithstanding those analogies."—J. M. C.

Atmometry.—The desirability of having an atmometer so constructed as to indicate the magnitude of the atmospheric evaporation power at any given moment is discussed by JOHNSTON and LIVINGSTON.[15] Attempts to produce such an instrument are described, but so far it has not been possible to overcome certain difficulties in converting evaporation power into pressure. The nearest approach to such an instrument which has proved successful is a device which permits two readings to be made with a very short time period between. An atmometer cup is mounted over a reservoir from which it may be cut off at will by means of a glass cock. It is also connected with a finely graduated burette from which the water will be drawn when the reservoir cock is closed. A reading can be made in a very short time at any desired intervals, and the average evaporating power for the period of observation can be calculated. Comparison of different environments is easily made.—CHARLES A. SHULL.

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[10] EVANS, A. W., Noteworthy *Lejeuneae* from Florida. Amer. Jour. Bot. **5**: 131–150. *figs. 5.* 1918.

[11] FERNALD, M. L., *Rosa blanda* and its allies of northern Maine and adjacent Canada. Rhodora **20**:90–96. 1918.

[12] PETCH, T., Additions to Ceylon fungi. Ann. Roy. Bot. Gard. Peradeniya **6**:195–256. 1917.

[13] WIEGAND, K. M., Some species and varieties of *Elymus* in Eastern North America. Rhodora **20**:81–90. 1918.

[14] BOWER, F. O., Studies in the phylogeny of the Filicales. VII. The Pteroideae. Ann. Botany **32**:1–68. *figs. 43.* 1918.

[15] JOHNSTON, EARL S., and LIVINGSTON, B. E., Measurement of evaporation rates for short time intervals. Plant World **19**:136–140. 1916.

Embryo sac of Oenothera.—ISHIKAWA[16] has published a very full account of the behavior of the gametophytes and the fertilization phenomena in *Oenothera nutans* and *O. pycnocarpa*, as well as in their hybrids. These two species were formerly included in *O. biennis*. The embryo sac arises from either the chalazal or micropylar megaspore, and often both develop simultaneously into complete embryo sacs. The sac is tetranucleate, lacking the antipodals and one of the polar nuclei. In fertilization one of the male nuclei fuses with the remaining polar nucleus, resulting in diploid endosperm. Self-sterility of some of the hybrids is due to feeble growth of the pollen tube. Tetranucleate embryo sacs occur also in *Ludwigia*, *Gaura*, *Godetia*, and *Circaea*.—J. M. C.

Iron in nutrient solutions.—CORSON and BAKKE,[17] working upon wheat and Canada field peas, have studied the relative merits of ferrous and ferric phosphates in nutrient solution. They find that iron in the nutrient solution is more important than generally considered; that ferric phosphate is more effective than ferrous phosphate, especially for wheat; and that ferric phosphate in the concentration suggested by SHIVE (0.0044 grams per liter) gives maximum dry weight.—WM. CROCKER.

Polyembryony.—HARVEY,[18] in connection with recording a case of polyembryony in *Quercus alba*, has given a summary of the recorded cases of polyembryony in angiosperms. The list includes 36 cases, scattered through "15 of the 49 alliances." In the case of *Quercus* reported two vigorous embryos occurred in the acorn, and it is of special interest because this is said to be the first reported case of polyembryony "in the first 13 alliances of the Archichlamydeae."—J. M. C.

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[16] ISHIKAWA, M., Studies on the embryo sac and fertilization in *Oenothera*. Ann. Botany **32**:277–317. *pl. 7. figs. 14.* 1918.

[17] CORSON, G. E., and BAKKE, A. L., The use of iron in nutrient solution for plants. Proc. Iowa Acad. Sci. **24**:477–482. 1917.

[18] HARVEY, LEROY H., Polyembryony in *Quercus alba*. Mich. Acad. Sci. Rep. 1917. 329–331.

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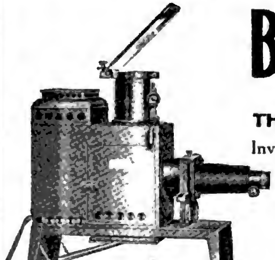

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THE

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SEPTEMBER 1918

SUSPENSOR AND EARLY EMBRYO OF PINUS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 242

JOHN THEODORE BUCHHOLZ

(WITH PLATES VI–X AND THREE FIGURES)

It has long been recognized that the embryos of plants furnish trustworthy morphological features for comparison in the study of phylogeny, but the surprising variations found in the proembryos of various gymnosperms have always been more or less of a stumbling block. This work was undertaken with the hope that a more critical study of the suspensor and early embryo of *Pinus* and of the phenomenon of polyembryony might prove of value in properly interpreting the rather flexible program that has been ascribed to this genus. Here it is, also, that we find a striking parallel to some of the early cleavage phenomena involved in the biology of twins in animals, a subject of some current interest to zoologists.

This paper will limit itself largely to such phases of the embryogeny of *Pinus* as were most effectively studied by means of a special technique for dissection, developed by the writer, and to a discussion of the relation of the early *Pinus* embryo to other conifer types. Certain phases of the later embryo will also be described, but the development of the internal features of the late embryo will be treated in another paper.

Historical

A summary of views in regard to the embryogeny of conifers is given by COULTER and CHAMBERLAIN (**10**), so that it will suffice to note those features in the historical development of the subject which concern our own investigation.

ROBERT BROWN (**2**), in discussing the similarities of the ovulate structures of cycads and conifers, mentioned his own observations of occasional polyembryony in conifers, which was known to be a constant feature in cycads. In a later treatise (**3**) he announced polyembryony as a constant feature among several genera of the Pinaceae and felt convinced that this feature is common to the entire family. He noted the origin of the embryos from "corpuscula" or "areolae," 3–6 in number, at the upper extremity of the "aminos" (endosperm), and pointed out that this provision of several "corpuscula" was like that in cycads, where it also made possible the development of several embryos. He called the suspensors "funiculi," finding that these frequently branch to form still other embryos.

MIRBEL and SPACH (**27**) announced their results from a careful study of several pines and also *Thuja* and *Taxus*, confirming the work of BROWN and extending our knowledge to other forms. In this account these workers were the first to use the terms "suspensor" and "rosette," although in their otherwise excellent figures they show 5 cells in each tier of the early embryo, 5 rosette cells, and 5 vertical rows of cells coming from the base of the corpusculum.

SCHLEIDEN (**36**) gave the first accurate general description of the development of the early embryo, beginning with the "embryonal globule" on the end of the suspensor. His views regarding the earlier stages of the embryo were confused by his erroneous conception that the pollen tube formed the embryo. He pointed out the correct order of appearance of the stem tip meristem and cotyledons, and gave a good account of the formation of the suspensor in its late stages after it becomes massive, describing it as an elongation of cells from the radical portion of the embryo.

HARTIG (**15**) was possibly the first to point out that the upper end of the suspensor is a single cell, but he regarded this cell as being of vegetative origin. He described a "nest of cells" from which individual cells elongate, and thought that the embryonal tip cell was cut off some time after elongation.

SCHACHT (35) agreed with SCHLEIDEN that the pollen tube enters the corpusculum and produces the embryo at its base. He described the rosette correctly as consisting of 4 cells instead of the 5 shown by MIRBEL and SPACH. SCHACHT described the 4 tiers of 4 cells each, known to us as the end product of the proembryo stage. He announced definitely that the 4 rows of cells in *Pinus Pumilio* always separate into 4 embryos and believed that they would split up further. In *Taxus baccata* and *Abies* he reported no splitting of the product of the corpusculum into several embryos.

GOTTSCHE (14) gives a critical review and confirmation of the facts known at the time and a more accurate description of the corpusculum, which he found to originate in some unpollinated cycads, and is therefore independent of the pollen.

HOFMEISTER (17) made a careful study of all stages in the development of the ovule and confirmed the facts then known. He pointed out how wonderfully simultaneous fertilization occurs in all the plants of the same species and how rapidly the proembryo stages are passed through. He was the first to regard the terminal cell of the early embryo as an apical cell. He thought also that the later embryo and seedling grow by means of an apical cell, and even believed he could demonstrate it in the adult stem tip of conifers.

PFITZER (32) denied the existence of an apical cell in the stem tip of conifers, but confirmed HOFMEISTER's work in regard to the existence of an apical cell in the early embryo, although he assigned to it only about 5 segments as a maximum for *Thuja*, and in Pinaceae he stated that the apical cell stage was even shorter. He calls attention in his conclusion to the fact that this may be taken as a case of embryonic recapitulation of the pteridophyte manner of development. He published no figures.

STRASBURGER (38) made a very careful study of the embryogeny of 8 or more genera of gymnosperms. In many particulars he corroborated the former accounts. His many excellent figures are accurate and most of them still useful. He denies the existence of an apical cell in all but the Cupressineae, where he found a definitely organized apical cell in the early embryo. In *Pinus* and other Abietineae he finds this stage omitted or not constantly present, an indication that these are less primitive than the Cupressineae. In the further differentiation of the embryo he goes into greater detail than any previous worker. In *Pinus* and *Picea* the plerome tip of the root is set off about 0.15 mm. from the apex of the cylindrical mass of cells which is now about 0.5 mm. long, measured to the point where the cells form suspensors. In the account, which he says is practically the same for all the conifers, the stem tip meristem is next in appearance, followed by the cotyledonary primordia which arise in a circle about this point. His description of the cotyledon and stem tip development is substantially the same as that of SCHLEIDEN (**36**). At this stage of development the embryo reaches the lower end of the endosperm, and further growth and elongation bring the radical end of the embryo back to the place of origin of the suspensor.

STRASBURGER states that the number of embryos beginning development may be as high as 20, all but one of which abort in various early stages of development. In *Picea vulgaris* he finds that the 4 rows of cells of the proembryo do not separate, but all 4 of the embryonal cells at the tip of the suspensor contribute to the formation of 1 embryo.

The accounts, by the early workers, of the proembryo stages differ widely. SCHACHT (**35**) shows correctly the completed proembryo when it consists of 4 tiers of 4 cells each with the upper tier open to the egg. STRASBURGER (**38, 39**) attempted to explain the stages between fertilization and this completed proembryo, but, like other early workers, he failed to recognize the nature and extent of the free nuclear divisions. CHAMBERLAIN (**5**) described some details in the development of the proembryo, and later COULTER and CHAMBERLAIN (**9**) figured a more complete series of these stages. FERGUSON (**13**) added still more, working on 6 genera of *Pinus*, and found, as did MIYAKE (**28**) in *Picea*, that the upper tier of 4 cells, in the 8-celled proembryo, divide before the lower. Later, KILDAHL (**19**) found both orders of division in

Pinus Laricio, between the upper and lower tier of this stage, and also made a detailed study of the order and manner of development of walls in the proembryo, a thing which had confused many previous investigators.

COULTER (**8**) and COULTER and CHAMBERLAIN (**9**) described some of the early stages in the developing embryo, and, like STRASBURGER, denied the existence of a true apical cell stage. They also stated that the lower tier of the proembryo may develop into a single embryo, or that the vertical rows of cells frequently become separated to form 4 embryos. One of these may even divide by a vertical wall and the 2 daughter embryonal cells become organically separated (**8**), developing subsequently as 2 separate embryos on the end of the same suspensor. This would give us a very fluctuating program of possibilities in the development of the early embryo of *Pinus*.

SAXTON (**33**), in a study of the embryo of *Pinus pinaster*, gives some of the stages in the development of the embryo between the proembryo and the ripe seed. He concludes that an apical cell stage exists, which develops several segments, and in one case shows an embryo which he estimates as one of 30 cells, which still has an apical cell. He describes as anomalous some of the ordinary stages, and his account is rather incomplete, in many respects less adequate than that of STRASBURGER (**38**), to which he does not refer. SAXTON also finds that "the cotyledon primordia are exactly equal and equivalent in their origin."

Investigation

MATERIAL AND METHOD

The cones of *Pinus Banksiana* were collected from the dunes near Miller, Indiana, during the summers of 1914 and 1916, at weekly intervals during the latter part of June, July, and August. Cones of *P. Laricio* were secured from the parks in Chicago in 1914 and 1916, and from Richmond, Indiana, in 1915. *P. sylvestris* was also secured with the Richmond collections, and *P. echinata* was collected at Conway, Arkansas, during the summers of 1914 and 1915.

The embryos were removed from the ovules in the living condition by dissection under water, and these embryos with their suspensor systems were stained and mounted as permanent preparations. Studies were also made from serial sections cut in paraffin, but most of the drawings accompanying this paper were made from the dissected preparations mounted in Venetian turpentine. The latter were found to be superior to anything else for a study of the coiled suspensors and the further development of the rosette.

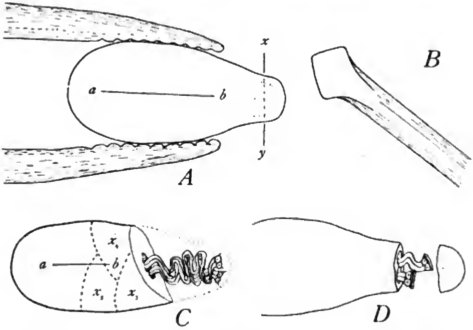

Fig. 1.—Illustrating methods of holding and dissecting pine ovules

Dissection.—The dissection must be done with living material under a dissection microscope, or preferably under a binocular microscope with magnification of about 20. The gametophytes are removed from the testa and placed in water in a watchglass. A very useful tool for the dissection, which must be executed under water, is a needle whose point has been flattened and ground to form 2 cutting edges, as shown in *B*, text fig. 1. The naked gametophytes, after being removed from the ovule, are held with forceps in the position shown in text fig. 1, *A*. Frequently the nucellus may be found, resembling a thin cap over the end of the gametophyte, and must first be removed, and sometimes the gametophyte may still be surrounded by the thin inner testa. The forceps with which the gametophytes are held should be small and have weak springs, in order to avoid crushing the tender tissue. With the dissecting tool *B* the end of the gametophyte is removed along the line *xy*. By teasing a little deeper into the tissue around the edges of the archegonia it is possible to loosen the embryos at the bases of the archegonia, allowing the rosettes to be pushed out by the suspensor as in *D*, text fig. 1.

Usually a little gentle stroking with slight pressure in the direction *a* to *b* with the dissecting instrument held nearly horizontal (to avoid crushing the tissue) is sufficient to loosen the embryo and gradually force it out. A slight pressure with the forceps on the sides of the gametophyte at the proper moment may help. Sometimes gametophytes must be split vertically along the line *ab* before the older embryos can be removed.

When the embryos are imbedded more firmly, it may be impossible to dislodge them by these methods. Sometimes it has been found possible to remove embryos with the complete suspensor system by chipping away pieces of the gametophyte, first from one side and then from the other. This is accomplished most easily by rolling the gametophyte over after each chip has been removed, cutting off pieces x_3 x_4 x_5 (text fig. 1, *C*) alternately, until the embryos are sufficiently loosened. Any method of pulling the embryos out by taking hold of the upper part of the suspensors without first loosening the embryos below results in an incomplete embryo and suspensor system. In spite of the greatest care and perseverance it is often impossible to remove the suspensors and embryos without some of the latter breaking off. Which of the preceding methods is to be used will depend somewhat upon the condition and stage of development of the embryos.

In the earlier studies, which were carried out in this manner, many embryos were found abnormal, in which the protoplasts had escaped from the cells and could be found as dark staining masses near the empty cells. Careful study revealed the fact that this was an osmotic phenomenon, due to the fact that the dissection was executed under water. The cells have a high osmotic pressure, and when placed in water they swell and break in a short time. This may be avoided by dissecting the embryos out under a 0.3 gm. molecular sugar solution. This strength of solution is still low enough to allow the cells to become fully turgid, and was found satisfactory for a number of species. Doubtless the strength of solution required will vary somewhat with the species and with the condition of the material.

KILLING AND STAINING.—After removal the embryos may be transferred to the killing fluid by means of a pipette with a 2 mm. opening. A good fixing agent is 6 per cent formalin in 50 per cent alcohol, and it is at the same time an excellent preservative in which they may be kept indefinitely, but aqueous formalin alone is not satisfactory. The embryos should be washed through several changes of water before staining, and may be transferred directly to water from the solution. The staining was done in saltcellar watchglasses with Delafield's haematoxylin or safranin. The haematoxylin was used for most of the preparations and was diluted to one-half of its usual strength. The water is removed with a pipette and a few drops of the stain applied for 5–10 minutes, which will stain them very deeply. At this point one of the most difficult steps is encountered, namely, to prevent losing the material while the stain is being removed. It was found best to dilute the stain with water until the watchglass is full. The upper layers of the solution may now be removed without disturbing the embryos at the bottom, but great care must be exercised to prevent losing the embryos, and the material should be watched as the pipette is filled by holding it over an illuminated white surface, as on the stage of a block dissecting microscope. More water is added and the operation repeated until the liquid is clear.

The overstained embryos are now de-stained with acidulated water (about one drop of HCl per 200 cc. of water). The stain is extracted slowly and must be watched over a low power microscope. The de-staining should be continued until the cytoplasm is well differentiated from the nucleus in the embryonal cells at the tip, and the suspensor cells should still be slightly blue. Very thorough washing is necessary to remove all traces of the acid or the preparations will fade. If safranin is used, it is advisable to overstain and then extract the stain to the desired point.

Mounting.—After the last washing 10 per cent glycerine is added and the material set aside to evaporate in a place protected from dust. When the concentrated glycerine is washed out with 95 per cent alcohol, great care must be exercised to prevent injury to the preparation. Several changes of alcohol will be necessary to remove all the glycerine, and after washing twice in absolute alcohol the 10 per cent Venetian turpentine is added and the watchglass placed in a desiccator. It is not desirable to allow the Venetian turpentine to get too stiff, as the specimens will be broken in mounting. If more of the 10 per cent Venetian turpentine is added to thin it down, as is frequently done, it causes the cells to swell, the cell walls separating from the protoplasts, leaving a permanent clear space between. If the Venetian turpentine must be thinned down, it should be done by adding about 85 per cent Venetian turpentine. The preparations may be picked up for mounting by means of a needle with a curved point, or a spear point. In handling them they should be picked up in a drop of Venetian turpentine and not by attempting to pull them out.

Preparations were also made by changing the embryos from concentrated glycerine into glycerine jelly. These mounts were not very satisfactory and compare very unfavorably with those prepared in Venetian turpentine.

Methods for serial sections.—The ovules were prepared for the fixing agent by removing the testa completely from the gametophytes. This can be done without crushing the latter by slicing away one side of the ovule down to the gametophyte with a sharp scalpel, then slicing away the edge, whereupon the gametophyte may be pried out without injury by inserting the point of the scalpel under it. For the early proembryo stages it is not necessary to remove the gametophytes from the testa, but a slice should be cut from one side, or better from opposite sides, to permit good fixation. The older testa cuts with difficulty, and it was not possible to get good sections of *P. Banksiana* when the coat had been left on in stages after the early elongating suspensor.

The naked gametophytes were removed and placed for 20–30 hours in the killing fluid, consisting of a chromic-acetic mixture ($\frac{2}{3}$ per cent chromic, 1 per cent acetic). After washing overnight in running water they were dehydrated through a close series of graded alcohols, as follows: 5, 12, 20, 35, 50, 70, 85, 95, and 100 per cent. The xylols were also graded, but less closely: 15, 30, 50, 70, 85, and 100 per cent. The material was infiltrated with paraffin by adding the latter a little at a time, and preventing actual contact of the paraffin with the material by means of a perforated cardboard shelf fitted into the vial, a centimeter above the material.

Longitudinal and cross sections were cut serially 10 μ thick and stained by the usual methods employed for iron-alum haematoxylin. A counterstain of gold orange was found very effective in bringing out the otherwise transparent walls. The gold orange is dissolved in the clove oil to saturation. This is then decanted off and about one-fourth the volume of fresh clove oil added. This solution is poured on the slide after it has been stained and cleared in xylol. Only about a minute is necessary to stain the walls; if continued longer it colors the cytoplasm also. The gold orange has a great tendency to crystallize out as the oil evaporates, especially if the stain is too highly saturated. It is therefore advisable to rinse the slide with clove oil, followed by xylol.

In more recent work it was found that very brilliant preparations may be stained with safranin and light green as follows: the safranin must be a concentrated solution in 50 per cent alcohol (a full strength stock solution was used), with the sections left in it 1–3 days. After a rapid washing in 50, in 80, and then in 95 per cent alcohol the sections were placed in light green (about 1 per cent in 95 per cent alcohol) 2–5 minutes. The time for the action of the light green varies with the age of the material, the strength of the stain, and the length of time the sections were stained in safranin. It is desirable, therefore, to stain all the sections of one collection at the same time, and not to mix several collections in one staining. One or two trials will enable one to determine how long to leave the sections in light green, and the remaining slides may be carried through by this time schedule. If left in light green too long, the safranin will be washed out of the nuclei, and if taken out too soon the light green is not impregnated in the cell walls sufficiently to give the desired brilliant contrast. From light green the slides must be transferred rapidly through 95 per cent alcohol, absolute alcohol, alcohol-xylol, into xylol. The de-staining process is not checked until the sections have reached the pure xylol solution; thus only a short dip should be given into each solution. Although safranin with gentian violet, Delafield's haematoxylin, and iron alum haematoxylin with light green were all tested, they were found much less satisfactory than the iron-alum haematoxylin with gold orange or the safranin with light green.

FORMATION OF CORROSION CAVITY WITHIN GAMETOPHYTE

The first change that is noticeable in the tissue below the archegonia is a starch deposit, which appears in the cells of this region about the time of fertilization, or a few days later. In the living gametophyte this deposit makes the tissue appear opaque, and it gradually spreads down into the central part of the gametophyte until this white opaque region comes to occupy a funnel-shaped region extending downward from the archegonia. About the time the embryos break through the bases of the archegonia the cells at the center of this opaque region break down, at first in the large part of the funnel nearest the archegonia. This forms the beginning of the corrosion cavity, an opening which, as it enlarges, assumes the shape of a slightly flattened trumpet. At the same time the starch-containing zone enlarges and becomes more conspicuous.

Sections like that shown in fig. 1 indicate clearly that the digestive action of an enzyme on the endosperm doubtless precedes the elongation of the suspensor. The embryo is soon pushed so far into this cavity by the elongation of the latter that further elongation can only bring about its well known coiled and twisted condition. The importance of this mechanical action of the suspensor in keeping the embryo pressed into the bottom of the corrosion cavity is better realized when one tries to dislodge some of these embryos by dissection.

Many ovules were examined in which the gametophytes had well developed corrosion cavities, yet no traces of embryos could be found in them, indicating that the archegonia may secrete the digestive enzymes to form the cavity even though the eggs have not been fertilized. Many sections of this kind may be found in the collections of ovules made from one to two weeks after fertilization. These soon dry up and wither away within the hardening testa, so that one would not include them in the later collections of material if the testa is first removed.

The subsequent enlargement of the corrosion cavity to accommodate the growing embryo is unquestionably due to digestive enzymes secreted by the embryo itself. The archegonia disappear as recognizable structures soon after the primary suspensor has fully elongated. The rosettes are usually found pressed against the top of the cavity, which now includes the space occupied by the archegonia after the latter have broken down. An unfertilized archegonium withers away soon after the formation of the corrosion cavity, its place being marked by a shrunken chip of hardened protoplasm which is often molded into the shape of the lower portion and side of this organ. Later this disappears also.

EMBRYO DEVELOPMENT

This investigation takes up the development of the embryo beginning with the 16-celled stage, which has generally been recognized as the end stage of the proembryo. It is necessary, however, to consider some of the well known earlier stages, and for these facts we will depend upon the results of previous workers which have been reviewed in the historical discussion.

Of the 4 tiers of 4 cells each, the lowest constitutes the embryonal group, each of which is an apical cell of one cutting face; the next tier above constitutes the suspensor group, each of which elongates to form a primary suspensor cell; the third tier has been called the rosette, and its further development has never before been followed out; and the uppermost tier of cells, which have incomplete walls and are in open communication with the egg, sooner or later disintegrate. Fig. 1 shows a longitudinal section through the base of an archegonium after the suspensor cells have begun to elongate and before any of the cells of the embryonal tier have undergone further division. In fig. 38 the embryonal tier has given rise to a tier of cells (e_1) between it and the suspensor, and at the left in fig. 37 an embryonal cell may be seen in anaphase of division.

SUSPENSOR.—The tier of suspensor cells elongates and pushes the tier of embryonal cells into the cavity below. When the suspensor cells have elongated slightly more than in fig. 1, the embryonal cells give rise to the first embryonal tube initials (e_1), and by the time the suspensor cells have elongated to the stage shown in figs. 39 and 40 another transverse wall has appeared in the apical cell below, giving rise to e_2, the second embryonal tube initials. This is soon followed by the elongation of the first embryonal tube initials (fig. 6, e_1) to form tubes like the suspensor cells, the first embryonal tubes. This added part of the suspensor is the secondary suspensor.

Separation of the vertical rows of cells soon follows the division of the embryonal cells, although it may occur earlier, as is the case in fig. 37 at the left. In none of the species of pines studied was a single case found in which the 4 vertical rows of cells did not separate to form 4 embryos. It will be seen from a study of figs. 39, 40, 41, and 44 that the elongating first embryonal tubes are no longer in an even tier, and one of the embryos has already gained the lead in penetrating the endosperm. The struggle for supremacy between the 4 primary embryos of an archegonium is well shown in figs. 40, 41, and 44, while in figs. 43 and 45 two archegonia are concerned.

Since the primary embryos have now separated, we shall regard one of these 4 as the unit for discussion. One of the 4 suspensor cells and all of the cells formed below it by the embryonal cell constitute one primary embryo, while all the embryos produced by an egg will be spoken of as an embryo system.

It is evident from a study of the development of the early part of the suspensor that the primary suspensor tubes never divide to form other tubes or cells. Likewise, an embryonal tube never undergoes division after it has begun to elongate, but an embryonal tube initial cell may divide by a vertical wall before elongation, as e_2 in figs. 6, 8, 14, and 20, or e_3 in figs. 10 and 16. When the embryonal tube initial divides and gives rise to 2 or more cells in a tier, these elongate together into a collateral group of embryonal tubes (figs. 47–50), forming a suspensor division. These suspensor divisions are all parts of the secondary suspensor, but when they consist of 4 tubes, as in fig. 50, they look very much like the lower part of a group of primary suspensors. For example, if the e_3 group of fig. 50 were studied from sections only, with the upper part of the suspensors confused as they are in fig. 45 (making it impossible to trace any of the tubes back to the rosette), it would be natural to mistake this perfect suspensor division as the group of primary suspensors. It is quite possible that a study of such sections has given rise to the statement that in *Pinus* all 4 of the embryonal cells may contribute to the formation of 1 embryo, or they may form 4 embryos.

The initial cell for the second embryonal tubes (e_2) and for the third and subsequent embryonal tubes are cut off as segments of the apical cell, first by transverse walls, and later as oblique segments. The initial cell of an early embryonal tube may elongate into a 1-celled suspensor division, resembling a primary suspensor cell, or it may first divide by a vertical wall as e_2 in figs. 6 and 8. Fig. 16 shows e_2 as a single elongated cell and e_3 with 3 cells, while fig. 20 shows e_2 of 4 cells. There is considerable variation in the number of cells found in the embryonal tube groups of corresponding suspensor divisions, and variations are frequently found among the individuals of the same embryo system.

After the initial cells of the embryonal tubes begin to divide by vertical walls and elongate to form the suspensor divisions, each succeeding bundle of embryonal tubes consists of more cells than the tier above it (figs. 46–52). Only one exception to this has been found among the 500 or more dissected preparations of various pines, and this one was *P. Laricio*, shown in fig. 24. Here *s* and e_1 (not shown) are single-celled, e_2 is of 2 cells, and e_3 again 1-celled, while e_4 and e_5 will undergo other divisions before beginning to elongate. Careful examination of many preparations indicates that the separation of the 4 primary embryos precedes the division of any of the embryonal tube initial cells by vertical walls.

The primary suspensor, that is, the first suspensor division, is often collapsed and withered by the time 4 or more divisions have formed. The upper parts of collapsed suspensors are shown in figs. 65 and 68, while fig. 46 still has a turgid primary suspensor. The primary suspensors frequently collapse in about the stage shown in fig. 46 or soon after, and the cells of the older portion of the secondary suspensor also collapse in turn, so that in an older embryo, like that of fig. 51, the upper part of the suspensor cannot be studied.

In order to determine the amount of variation in the early suspensor divisions, several hundred preparations of *P. Banksiana* were examined and the types of suspensor development noted.

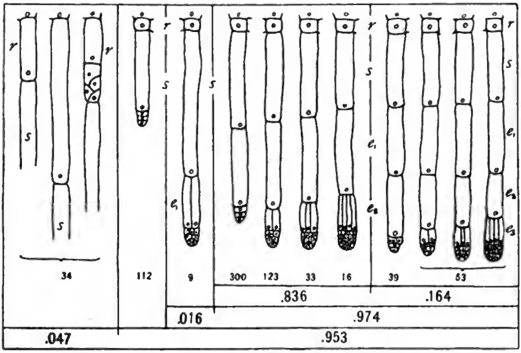

Fig. 2.—Graphic statistical summary of variations in early suspensor divisions of *Pinus Banksiana:* the figures indicate the number of examples of the various types of suspensors observed, and their distribution in percentage.

The results are summarized in the diagrams of text fig. 2. It was common in more than four-fifths of the cases examined to find the single primary suspensor followed by a 1-celled embryonal tube (e_1), this followed by 2 or more cells in the next suspensor division, after which the tubes interlock and elongate irregularly, as in figs. 47, 49, and 51. Less than one-fifth of the cases were found with the primary suspensor followed by 2 successive single-celled suspensor divisions and 2 or more tubes in the fourth suspensor division e_3. Only about 1.6 per cent of the embryos were found to have the first embryonal tubes or second suspensor division of 2 cells.

In nearly 5 per cent of the cases the rosettes were elongated to resemble suspensor cells.

It will be seen that the third embryonal tube group, or fourth suspensor division, always consists of 2 or more cells, and after this division or the one following the tubes begin to elongate and interlock to form the suspensor. The transition from the jointed to the interlocked and more massive portion of the suspensor is well illustrated by figs. 47, 49, 50, and 51.

The suspensor becomes more and more massive as the embryo increases in diameter. The embryo is first pushed as far as possible into the corrosion cavity by the mechanical action of the suspensor; later it remains nearly stationary in the lower end of this cavity, but continues to give off the suspensor by the successive elongation of the cells from the radical end of the embryo; finally, as the embryo develops to its full size, the radical portion again reaches the archegonial end of the cavity. As the root cap becomes differentiated in the embryo, it may be seen that this organ and the suspensor gradually merge into each other; in fact, the late suspensor is formed from the root cap by the successive elongation of layer after layer of cells.

ELONGATED CELLS.—The nuclei of the suspensor cells and embryonal tubes always seem to hold a definite size relation to the cells. A large suspensor tube may frequently contain a nucleus larger than an entire cell in the embryonal group at the apex. The position of these nuclei is always at the embryonal end of these tubes. More of the cytoplasm of the cell is usually found here, near the nuclei. The ends of these cells containing the nuclei are frequently enlarged considerably. Often one of the primary suspensor cells breaks loose at the lower end during elongation. Figs. 41 and 45 show such tubes which continued to enlarge at the lower end and formed a balloon, while fig. 42 shows an earlier stage in another tube. These phenomena are not uncommon.

BASAL PLATE.—A thickened plate (*p*) is deposited above the rosette soon after the suspensor begins to elongate. Something similar was found in *Podocarpus*, where COKER (**6**) calls it a cellulose plug, "a novelty among gymnosperms." It is called a "basal plate" by the writer because it is a plate rather than a plug, and its chemical nature in *Pinus* was not determined. The word "basal" seems fitting because it is, in a real sense, basal to the embryos in its position. Doubtless careful search will reveal this in many other gymnosperms. Whether the rosette is present as in fig. 41, elongated as in fig. 54, or absent as in *Podocarpus*, the basal plate is always formed in the egg cavity on the walls toward the embryos.

APICAL CELL.—A distinct apical cell stage exists from the time the embryo cells first have walls. In fig. 1 the suspensor cells (*s*) are the first segments of their respective apical cells (*a*). Here the 4 primary embryos are apparently still united; but if they may be looked upon as organizing distinct from each other, the 4 cells which gave rise to the lower 8 cells of the 16-celled embryo are embryo initial cells. The work of COULTER and CHAMBERLAIN (**9**), FERGUSON (**13**), and KILDAHL (**19**) has shown that these which we call embryo initial cells were formed in the mitosis between the 4-nucleate and 8-nucleate proembryo, the place where KILDAHL (**19**) found that the first walls appeared. FERGUSON (**13**) and KILDAHL (**19**) found that the rosette and upper open tier organize next, from the upper 4 nuclei (although KILDAHL found exceptions to this), and therefore this lowest tier of the 12-celled stage is a holdover since the first appearance of walls.

The second segment of the apical cell is the initial cell of the first embryonal tube. This segment, as well as the third and fourth, are formed by an apical cell of 1 cutting face. Figs. 1–6 all show apical cells of a single cutting face, while in figs. 7, 8, 9, 11, and 12 the first oblique wall of the apical cell has appeared. This wall is sometimes only slightly tilted, as in fig. 9, or it may be nearly vertical, as in figs. 10 and 14.

The stage at which this oblique wall first appears is not always the same. A large number of embryos of *P. Banksiana* were examined in order to determine the average condition in this respect. This study showed that these variations are somewhat similar to those found in the number of tubes in the early suspensor divisions. In nearly two-thirds of the cases the first oblique wall appeared after the primary suspensor and 2 embryonal tube initial cells (3 suspensor divisions) had been formed by the apical cell of one cutting face; one-fourth after 2 suspensor divisions; and one-tenth after 4 suspensor divisions had been formed.

It is often difficult to determine with certainty in an embryo like fig. 15, for example, at what stage the first oblique wall was formed. Here the last horizontal wall is tilted slightly, so one might think that this was modified by growth after the first oblique wall appeared; but it is also possible that this segment was first formed with a perfectly horizontal wall, and this later enlarged on one side to appear slightly oblique, so that the first real oblique wall is the one which appears nearly vertical. While these two interpretations could be given to fig. 15, in making the study referred to in the foregoing paragraph, the slightly oblique wall was looked upon as though it has been formed in an oblique position by the apical cell.

A stage in which the apical cell has 2 cutting faces does not exist, or it is so shortened that it cannot easily be recognized. Figs. 15 and 16 have only 2 oblique segments cut off, but these are probably the first 2 segments of the apical cell stage with 3 cutting faces. Apical cells with 3 cutting faces are found in embryos only slightly larger, such as figs. 17 and 18. Figs. 17–23 are all from whole mounts in Venetian turpentine and show pyramidal apical cells of 3 cutting faces.

Many irregularities are found in regard to the position of the apical cell. It is frequently so far to one side of the tip of the embryo that it might be overlooked in some serial sections. A section of an embryo like figs. 17, 20, or 28, if cut in another plane, would not show the apical cell so favorably, and might be mistaken for an embryo without an apical cell.

A very puzzling case is shown in fig. 21*a*, *b*. Fig. 21*a* shows the embryo in a high focus, with the shadows of nuclei of a lower focus shown by the dotted lines. Fig. 21*b* shows the nuclei and cell walls of the same as seen in low focus. This looks like an embryo which has no apical cell, and it is on the basis of very similar figures that STRASBURGER (**38, 39**), and other workers since, have denied the existence of an apical cell as a constant feature. In this particular instance the apical cell is at one corner of the lower tier of 4 cells. It is either the cell to the right in high focus, or the lower cell to the left. For instance, if it is the upper right cell, then either the cell below it or the one in the same plane of focus beside it is its last segment, while the remaining 2 cells together constitute the next to the last segment. The other cells of the embryo may well have arisen while the apical cell had 1 cutting face.

Fig. 13 shows a case very similar to fig. 21*a*, but somewhat younger. If the apical cell and the last segment shown here should both divide with walls in the plane of the paper, and the next tier of 2 cells above this (e_3) should do the same, it would not differ essentially from fig. 21*a*, *b*. Fig. 14 is in the same stage as fig. 13, but with the e_2 suspensor division elongated.

In longitudinal sections the apical cell and its segmentation may usually be seen (figs. 25–29). Fig. 31 is an embryo of about 200 cells, one of the smallest embryos that could be found without an apical cell, and fig. 30 is a larger embryo of about 275 cells, which apparently still has one. Fig. 32 shows a larger embryo of 750 cells which no longer has an apical cell; and figs. 35*a* and 35*b* show the first 2 sections through the end of an embryo in which the apical cell is replaced by a meristematic group. Figs. 34*a* to 34*d* are consecutive cross-sections through an embryo a little larger than that of fig. 32, in which the apical cell may still be found, probably in an arrested condition, before the meristematic group of cells has become active. Fig. 34*e* is a diagram combining sections 34*a* to 34*c* and showing the relation of the segments to the apical cell.

Figs. 33*a* and 33*b*, sections through the tip of an embryo slightly smaller, show an apical cell and segments as diagrammed in fig. 33*c*. This shows the segments arranged clockwise, while in fig. 34*e* they are counter-clockwise. This difference is easily accounted for, since the serial sections on these 2 slides run in opposite directions through the embryos. In fig. 34 the views of the cross-sections proceed toward the apical cell from the base of the embryo, while in fig. 33 they proceed from the apex inward. The segments thus appear in the same order on the embryo and proceed in the same direction as the thread of a wood screw, beginning at the point which corresponds to the apical cell and passing back along the thread toward the older segments. This is probably the usual arrangement of the spiral of segments, as no exceptions were found in an examination of several other cases, although no extensive study of this feature was undertaken.

The early apical cell forms a slightly compressed and slightly conical mass of cells. When the apical cell ceases to function, as in fig. 32, the embryo is more uniformly cylindrical, sometimes slightly club-shaped. The apical cell vanishes long before the stem tip, the cotyledons, or any of the body regions are recognizable, and nearly all of the early part of the embryo formed by apical cell growth goes to form the suspensor by the elongation of layer after layer of cells from the basal part of the embryo.

ROSETTE AND ROSETTE EMBRYOS

No investigator seems to have followed the development of the rosette further than through the early stages of elongation of the suspensor. That the open cells of the tier above the rosette disorganize has been stated by various workers. The writer has also been unable to find any traces of these nuclei of the upper open tier after the early stages of suspensor elongation, and doubtless they disintegrate.

The rosette has usually been regarded as a group of cells between the main body of the egg and the suspensor, having no particular function. This view has proved to be erroneous, for the rosette is a group of young embryo initials which will produce embryos. These embryos are bounded by thick walls and are not so free to elongate as the primary embryos below them.

After a little delay, during which the adjoining primary suspensor cells elongate, the rosette cells divide, as shown in one of the rosette cells of fig. 58, also in some of the rosette cells seen in polar view in fig. 59. A wall soon appears in one of the 2 daughter cells, inclined at an angle to the first (fig. 61, and rosette of fig. 46), forming the second segment of the apical cell. The apical cell continues to cut off segments on 2 or more sides, and the later embryo appears to have 3 cutting faces. Fig. 65 is a side view of a group of rosette embryos and shows well the apical cell and its segmentation, and (*s*) the upper portion of the collapsed primary suspensor.

None of the rosette embryos has been found to reach stages much in advance of those shown in figs. 64–68. In some of these the embryonal tubes elongating from the basal portion of the embryo have formed a recognizable suspensor, which often appears freakish, as in fig. 68, modified no doubt by the unfavorable position and the unequal thickness of the walls of the rosette cells.

It will be seen that the orientation of these rosette embryos is variable. In fig. 67 they have begun to elongate in various directions. The direction of the apical portion and the suspensor must be determined by the first few divisions, and figs. 59–64 show that these are likewise quite variable. Before the rosette embryos have developed much beyond the early stages, such as fig. 59, the archegonium breaks down, and these embryos may be found pushed up against the top of the corrosion cavity by the suspensor. Even before the archegonium has completely broken down the rosette is frequently tilted by the twisting suspensor below, and it is quite probable that the orientation of the rosette embryos is related to the position of the rosette when the first divisions occur in these embryo initial cells, a thing that may well account for the lack of uniformity or regularity.

It often happens that some of the rosette cells disorganize early and fail to produce embryos. Rosette cells may be found with no visible nuclei, or with nuclei in various stages of disintegration, while the neighboring rosette cells are producing embryos. While these exceptions occur, it is evident that the normal product of an archegonium is 8 embryos. This makes polyembryony a much more extensive phenomenon than has hitherto been recognized. All of the species of *Pinus* investigated showed this peculiarity, *P. Banksiana*, *P. Laricio*, *P. echinata*, and *P. sylvestris*. Rosette embryos develop less rapidly than the 4 primary embryos, abort in early stages, and it is entirely outside of the range of probability that they may ever contribute the embryo of the seed.

ELONGATION OF THE ROSETTE.—Another abnormal phenomenon that was occasionally noted was that of elongated rosette cells resembling the primary suspensors. Fig. 53 shows a rosette in the first stages of elongation; fig. 54 shows another that is well advanced. Elongated rosette cells were found in nearly 5 per cent of the total number of preparations examined in connection with the study summarized in text fig. 2.

A condition which demonstrates that these rosette cells are potentially embryos, even when they elongate to form suspensors or embryonal tubes, is shown in fig. 54, in which a mitotic figure may be seen in the lower portion of one of these elongated cells. Fig. 55 shows this mitotic figure of fig. 54 enlarged. An ordinary suspensor cell or embryonal tube has never been found to undergo division after elongation. The origin of the cells intermediate between the elongated rosette and the primary suspensor of fig. 56, and of 1 rosette in fig. 57, seemed a puzzle until the case shown in fig. 54 made it apparent that these cells may arise from the rosette tube. They are terminal cells of the rosette embryos that were formed after the rosette cell had begun to elongate. The rosette cell at the left, in fig. 53, has a nucleus in spirem stage, probably preparing for the first mitosis in the formation of an elongated rosette embryo of this kind.

POLYEMBRYONY

In *Pinus* polyembryony is a much more extensive phenomenon than is generally known. Since the rosette produces 4 embryos, and 4 others are always produced by the splitting of the lower primary embryos, 8 embryos may be formed from each fertilized egg. The greatest number of embryos possible is 8 times the number of archegonia, which might reach as high as 48 if all 6 of the archegonia, present in some species, were fertilized. Fertilization must be very nearly simultaneous in all the archegonia, and other conditions very favorable if the maximum number of embryos is to be produced. Fig. 69 shows an embryo complex, which had a delayed start and was stunted from the beginning, a condition which is frequently found where more than 3 archegonia are fertilized, with 1 more or less delayed.

In the various pines studied, 4 is the maximum number of embryo sets that were actually found, each related to one of the 4, 5, or 6 archegonia. Two or 3 archegonia were the usual number fertilized. In *P. Banksiana*, with only 2 or 3 archegonia, as large a number is not possible as in *P. Laricio*. Since the cones of the material studied were poorly pollinated, as was indicated by the relatively few good ovules and seeds developed per cone, no doubt the maximum possible number of embryos was not to be found in these collections.

The terminal embryo of the group is the successful one in the struggle for supremacy among the embryos. In very exceptional cases the successful embryo has been found to be the second one instead of the terminal. Occasionally an embryo develops with the reversed orientation, and the abortive embryos are frequently found in this reversed position.

Cases were also found where less than 4 primary embryos were produced from an archegonium, where one of the vertical rows of cells was aborted with little or no elongation of its suspensor, or the embryo initial cell itself was aborted. This condition might give the impression that one of the 2 or 3 primary embryos is composed of 2 vertical rows of cells that failed to separate in the normal way, were it not for the fact that when one of the embryos aborts in this way there are less than 4 suspensor tubes or first embryonal tubes.

No embryos have been found to arise from 2 or more vertical rows of cells combined. Such an embryo would have 2 apical cells, and wherever an embryo possesses a single apical cell and looks normal in other respects it is safe to conclude that it has come from one of the 4 embryonal cells. Another simple criterion is that of tracing the suspensor back to the rosette. If an embryo could be found attached to 2 primary suspensor cells, without the possibility that an embryo has been lost in dissection, it would indicate that 2 primary embryos were combined, but in this case the embryo should also have the appearance of being double, and the number of embryos present in the complex should be one less than the usual number. The writer found several cases which he suspected to be double embryos, but when they were more carefully studied they failed to fulfil these conditions.

TWINS.—So far as I have been able to find, no embryos arise by a further splitting of one of the 4 primary embryos. Since the terminal cell of the early embryo is an apical cell, an equal splitting could only occur after the formation of a vertical wall, as in figs. 10, 13, 14, and 15, and no cases of "twin embryos" formed by such a vertical splitting could be found. The embryos never even show tendencies to round off at these nearly vertical cleavages, or upon the formation of any wall other than the one which separates the 4 primary embryos. Such "twins" would be easily recognized in dissected preparations, since they would be found attached by their secondary suspensors to a common suspensor, leading back to a single primary suspensor cell.

When the 4 primary embryos are sectioned in stages before they are completely separated, it is possible, in rare cases, that 2 embryos may be so cut as to appear to be at the tip of a single suspensor or embryonal tube. This might look as if the 2 embryos had arisen on the end of the same suspensor by the splitting of a single one, especially if some of the adjoining sections are lost. The writer had the opportunity of examining the original slide from which the drawing of a "twin embryo" had been published (**8**). Upon critical examination it proved to show traces of the wall of a second suspensor cell from which the stain had been washed out, and is more correctly shown in fig. 36. One of the adjoining sections, which happened to be a very thick one, is missing from the slide. It was possibly lost off during the staining, as the accidentally thick sections of a series often are, but the recognition of this second suspensor cell gives each of the 2 embryos in this figure its own suspensor and indicates that these 2 embryos were 2 of the primary group of 4, sectioned in a rather unusual position. The possibility that one of the 4 primary embryos could split to form 2 has been claimed by several investigators, but no other figures showing twin embryos of pines could be found in the literature on this subject.

Another type of twins is that found when 2 of the members of the embryo complex develop to fair size to form the mature seed embryos. Although polyembryony is such an extensive phenomenon in *Pinus*, the writer has never been able to find a mature seed with 2 fully and equally developed embryos; one was always considerably larger than the other, and these were not very common. When these 2 embryos are members of the same embryo system, the twin formation is due to a cleavage phenomenon, and is similar to that of duplicate twins in animals.

THE LATER EMBRYO

In embryos of *P. Banksiana*, the size of fig. 47, the apical cell may usually still be found, but by the time the stage shown in fig. 51 is reached it has disappeared. The cylindrical mass of cells enlarges, and about the time the stage shown in fig. 52 is reached the cells near the tip begin to organize into an arch, shown by the dotted line of text fig. 3*A*. Under this arch is the plerome of the root tip, the first body region to appear. The periblem organizes outside of this dome and is thickest above it on the side toward the suspensor, where it merges with the tissue of the massive root

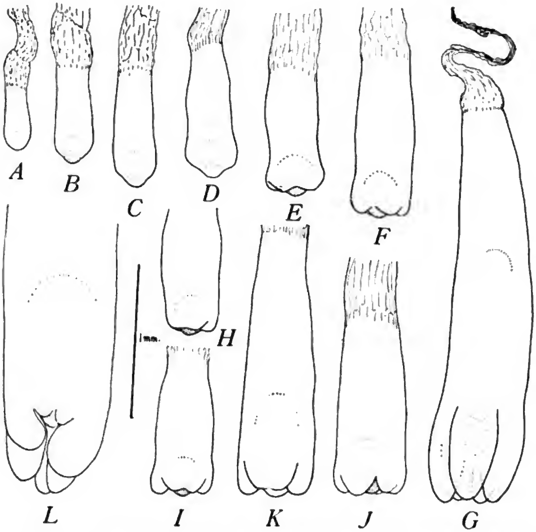

FIG. 3.—Development of stem tip and cotyledons; dotted line represents plerome of root tip; shaded area, meristem of stem tip; *H*, *I*, *J*, *K*, fusing cotyledons.

cap. This curved cell arrangement may be recognized in the whole embryos mounted in Venetian turpentine or balsam, but sections show the details of this cell organization much better.

The stem tip may be recognized as a slight protuberance in the position formerly occupied by the apical cell, but long after this cell has disappeared. It may first be seen in embryos about 175 $\mu \times 400$ μ; and in living embryos dissected out under water a transparent area develops in the tissues near it, which is shown by the shaded area of *B*, text fig. 3. The embryo enlarges, and by the time it has reached the size of *D* the circle of cotyledonary primordia is recognizable. The number of these primordia, like the number of cotyledons, is not constant, and ranges from 3 to 7. Although the cotyledonary primordia are usually equally developed when they first appear, sometimes they are larger or appear sooner on one side than on the other. Figs. *J* and *K* show cases where 2 primordia formed only 1 cotyledon. Figs. *H* and *I* show the same thing in earlier stages, and since stages older than *K* do not reveal a double tip on the broad cotyledons it is doubtless rapidly outgrown. Many broad cotyledons may have a similar origin, but some of them seem to arise directly from 1 broad primordium. Although embryos like *H*, *I*, *J*, and *K* are not as common as *E* and *F*, those that do not show fusing primordia, there is no doubt a distinct tendency in *P. Banksiana* to reduce the number of cotyledons. The mature embryo frequently has only 3 cotyledons, and 4 or 5 are the usual numbers. In *P. Laricio* fusing primordia were not found, but here there are usually 10 or more cotyledons, and there seems to be no tendency to reduce their number.

The embryos of these 2 species show a tendency to grow slightly zygomorphically. In some cases this seems to date from the first appearance of the primordia. It is usually not very pronounced, but an embryo of *P. Laricio*, extremely abnormal in this respect, is shown in text fig. 3*L*. Here the suppression of the cotyledons on one side is nearly complete, a condition which, in the presence of a cotyledonary tube, would result in an embryo similar to the monocotyledonous embryo, as described in recent work (11). Although 2 primordia sometimes combine to form a single cotyledon, none of these pine embryos have a cotyledonary tube at any stage of their development.

ABNORMALITIES

Among the seeds of *P. Banksiana* one was found in a germinated lot which had developed in the reversed position. The cotyledons and hypocotyl were protruding about 15 mm. from the micropylar end of the seed, while the root tip was imbedded in the endosperm. It died without developing much beyond this stage. Some of the aborted embryos of the pine seed are frequently reversed, and LAND (**20**) described a young embryo of *Thuja* which was directed toward the micropyle. Embryos matured in this position are very rare; this case which was germinated was the one case of the kind found in connection with this investigation.

Among the many hundreds of ovules from which the testa was removed preparatory to dissection or imbedding, many cases (at least 15) were found with 2 gametophytes in the same ovule. They occurred in two ways, end to end and side by side. The end to end gametophytes often joined obliquely, and each gametophyte is necessarily formed by the functioning of 2 megapsores. Whether these gametophytes belonged to the same tetrad row or to different tetrads is a matter of conjecture, but one would think that the side by side and obliquely joined prothallia have more probably developed from megaspores of different tetrads. *P. Banksiana*, which was most largely dissected, yielded the most of these double gametophytes. Several were also found of *P. echinata* and two of *P. Laricio*. It is not surprising that a very primitive conifer like *Pinus* should occasionally show this feature.

A few ovules were found in which the terminal embryo aborted and the second one dominated over the others, which is very unusual. Two seeds were found which contained 2 embryos, but in each case the embryo pair was quite unequally developed.

One sectioned ovule of *P. Banksiana* was found in which the customary splitting of the embryo complex did not take place as completely as usual. By a careful study of the series it is clear that each of the 4 embryos is pursuing its own independent development and has its own apical cell. One of the 4 embryos is clearly the largest and will no doubt dominate over the others quite as well as if they were more completely separated.

Discussion

APICAL CELL.—STRASBURGER (**38**) was the first to cast doubt upon the existence of an apical cell in the embryo of the Abietineae. He felt doubtful of it because it did not appear to be a constant feature. The instances in *Pinus* described and figured by him in which he considered the apical cell absent are practically the same as some of the more unusual ones described in this paper. He regards embryos like figs. 13, 14, and *21a* as having no apical cell; and while he recognized that in embryos like figs. 16 and 18 an apical cell seems to be present, he considered this apical cell growth not constant and that it has no phylogenetic significance.

COULTER (**8**) expresses the opinion that an apical cell is only simulated in *Pinus* and does not in reality exist. He is probably misled by the appearance of nearly vertical oblique walls in the terminal cell and by embryos like figs. 13 and *21a*. COULTER and CHAMBERLAIN (**9, 10**) do not mention an apical cell, and thus imply that such a stage does not exist, but point out that the problem of the development of the pine embryo after the first few divisions is an open one.

SAXTON (**33**) overlooked STRASBURGER'S work (**38, 39**), and although COULTER had expressed the opinion that an apical cell is only simulated, he is inclined to regard the terminal cell of the *P. pinaster* embryo as an apical cell. When he failed to find an oblique spindle he seemed not fully convinced about the existence of a true apical cell, which he figured only in young embryos up to 30 cells. For these reasons the writer considered it necessary to give considerable study and attention to the proof of the existence of an apical cell in the early embryo.

A series of embryos (figs. 9, 7, 8, 10, 13, and 14) may be selected showing the first oblique wall in all positions, from nearly transverse to vertical. This variation in the first oblique wall has made an occasional embryo hard to explain as having an apical cell. Fig. 15 shows how the next wall comes in, and after this stage the apical cell may easily be found, except that it is frequently very much to one side. The apical cell cuts the first oblique segment at no fixed stage, but probably at the time when the embryo is well separated from its neighbors in the embryo system. This same cause may also account for the variation in the time of appearance of the vertical walls in the initial cells of the early embryonal tubes.

STRASBURGER (**38**) also cites the case of an embryo similar to fig. 21*a* as disproving the constant existence of an apical cell, but fig. 21*a* has an apical cell; it is one of the 4 cells of the apical tier, one of the adjacent cells is its last segment, while the two remaining cells constitute the next older segment.

An embryo like fig. 21*a*, but in which the e_2 tier of cells has elongated, looks so much as though it shows the original 4 embryonal cell rows going into a single embryo that doubtless this impression could be created from a study of serial sections only. When STRASBURGER found a stage very similar to fig. 21*a*, however, he was able to trace the suspensor back to a single tube and recognize that it is only one-fourth of the product of the egg. According to his explanation the embryo from this stage on develops like that of *Picea*, in which the whole of the fertilized egg unites to form 1 embryo, and has no apical cell. All of my investigations have failed to support this view, but, on the contrary, embryos slightly older than fig. 21*a*, such as figs. 16, 18, 22, and 28, always have an apical cell, and this cell may usually still be found in embryos of 500 or more cells.[1] Certainly the instances where the apical cell cannot be found in embryos having several hundred cells or less are rare, and the most exceptional cases found in this investigation have been figured and described. Every essential condition for an apical cell is satisfied. It has the proper position on the embryo, being at or near the apex of a body with polar differentiation; it has the same general shape as the apical cell at the stem tip of a fern; and it has recognizable segments which may be related in their regular turn to the 3 cutting faces, even in some embryos of 800 cells.

From a comparative study of the embryos of other conifers it is probable that this apical cell feature is retained more generally than one would suppose. According to STRASBURGER (**38**) the Cupressineae all have this feature. COKER's (**7**) study of the embryo of *Taxodium* does not conflict with this view, for in many cases he was able to determine the succession of walls in young embryos, which suggests the possibility that an apical cell may be found here. In *Podocarpus* COKER (**6**) figures a number of embryo stages, some of which may have an apical cell; in others it appears doubtful. ARNOLDI (**1**) and LAWSON (**22**) show figures for the early embryos of *Sequoia* and *Sciadopitys* in which the embryonal cell has formed 1 or more vertical walls, a condition which precludes the possibility of an apical cell, according to the views of some investigators. However, according to the later stages of *Sequoia*, figured by SHAW (**37**) and ARNOLDI (**1**), an apical cell arrangement exists, and it is possible that the vertical walls were only the first obliquely placed walls of the apical cell, a condition which occurs occasionally in *Pinus*, and is explained in connection with figs. 13, 14, 15, and *21a*. SAXTON (**34**) shows some of the stages in *Actinostrobus* which are suggestive of an apical cell, and doubtless it may be found in many of the conifers. It is just as certain to be absent, even in some of the Abietineae, if STRASBURGER'S account of *Picea* (**38**) is correct, for if all 4 cells of the lower tier of the proembryo together produce an embryo, the apical cell loses its identity from the start.

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[1] Estimated roughly by counting the average number of cells in diameter and length and applying the formula $l\pi r^2$.

It is evident that in *Pinus* a primitive condition is found, in which the apical cell is still functional for a considerable period, and that in some derived conifers this has been retained more or less, while in some evolutionary lines it has been suppressed or completely eliminated.

APICAL CELL IN RELATION TO PROEMBRYO.—One of the great difficulties in accepting the apical cell as having phylogenetic significance has been the impression that if such a stage may be found it does not exist from the start. In looking over the literature it is apparent that many workers do not recognize an apical cell as such, unless it cuts off oblique segments from several cutting faces. Their apical cell would begin only with the first oblique wall. By studying the behavior of the segments in forming the suspensor the writer has shown that the embryonal cell is a hemispherical apical cell of a single cutting face, and that the primary suspensor cell is its first segment. We need not expect to go farther back in the proembryo than to when the embryo initial is organized; the stage previous to this is a free nuclear division which organizes these several equivalent cells. Thus the proembryo stage in *Pinus* is the stage in which the divisions occur that bring about cleavage polyembryony.

PROEMBRYO.—The free nuclear division which occurs after the 4 nuclei descend to the bottom of the egg is followed by walls which are complete for the lower tier of cells, but leave the upper tier in open communication with the egg. Thus, when the upper tier divides to form the rosette and the open tier above it, the cleavage is still essentially a free nuclear division. According to FERGUSON (**13**) and KILDAHL (**19**), this upper tier of the 8-celled proembryo usually divides before the lower, and in the resulting 12-celled stage all of the cells with complete walls, namely, the 8 cells of the lower 2 tiers, are embryo initials, which henceforth grow by means of an apical cell. This fact suggests the possibility that the upper open tier may also represent a tier of similar initials which has become abortive. This seems probable when we consider that in *Pinus* the lowest tier produces embryos immediately; the rosette tier only after some delay, and then not always; while the upper open tier represents a group of initials that failed to organize. The presence of this upper abortive tier suggests a reduction from a more extensive form of polyembryony.

The lower tier of the 8-celled proembryo sometimes divides before the upper one, according to KILDAHL (**19**), who also confirms this order. No proof exists that the upper tier ever undergoes another division when the lower one divides first, and it is possible that the nuclei shown in her fig. 11 would have collapsed without undergoing further divisions. This would give us, in this case, only 8 embryo initials instead of 12 (counting the upper open tiers as potential embryo initials), of which only 4 function. It seems evident that this order of division is rather uncommon. According to the interpretation that the embryos are separately organized by means of initial cells in the proembryo, the latter stage has a new significance as a real preliminary stage in the embryogeny. However, the proembryo stage should be considered closed in *Pinus* when the 12-celled stage is reached, rather than the 16-celled stage, and in the instance shown by KILDAHL the proembryo is complete in the 8-celled stage. Thus far "proembryo" has been recognized largely as a term of convenience to describe the stages preceding the elongation of the suspensor.

POLYEMBRYONY.—The writer has found it necessary to distinguish between the polyembryony caused by the simultaneous fertilization of several eggs and that brought about by the separation of the embryos of a single egg. The latter form of polyembryony, which is spoken of as "cleavage polyembryony," is no doubt a constant feature of *Pinus*, and may possibly be found in some of the other genera of this family. The statement that "all 4 cells of the lower tier may unite to form a single embryo, or they may separate to produce 4 embryos," may hold for the Abietineae as a group. The writer has found separated primary embryos in all of the species of *Pinus* examined, which includes *P. sylvestris*, for which STRASBURGER reports only 1 embryo per archegonium. Forms like *Thuja* (**20**) seem to show splitting of the embryos at times, while in other cases the archegonium produces only 1 embryo. COKER (**7**) found the embryos splitting apart in *Taxodium* and also in *Podocarpus* (**6**). Some of these more modern forms are therefore not constant like *Pinus* in this respect.

Polyembryony by cleavage from 1 egg is no doubt a primitive gymnosperm character, even though it has persisted to the *Ephedra* level, where it is on its way to elimination. No angiosperm has shown this form of polyembryony, which is a further proof that it is a primitive character. Aside from its phylogenetic significance, the feature of polyembryony is a wonderfully effective means for the possible elimination of unfit embryos, involving as it does in *Pinus* some 32 embryos when 4 archegonia are fertilized.

Although no matured twins have been found to arise by the cleavage of the egg in *Pinus*, this has been demonstrated for *Ginkgo* by LYON (**26**). Here we have a close parallel to the animal twins which are formed by cleavage, and LYON has shown that the twin embryos may originate from the same archegonium, remain organically connected, and develop equally to the maturity of the seed.

EARLY EMBRYO IN RELATION TO OTHER CONIFER EMBRYOS.—The known stages of the proembryos in *Picea* (**28**), *Abies* (**29**), *Pseudolarix* (**30**), and *Tsuga* (**31**) are reported as similar to *Pinus;* the embryo is said to consist eventually of 4 tiers of 4 cells each.

In *Sciadopitys* LAWSON (**25**) found 8 free nuclei before organization into tiers takes place. This is very significant, for here we may have this extra free nuclear division result in more embryo initials, a thing which would bring about a greater display of cleavage polyembryony than in *Pinus*. Judging from the figures of ARNOLDI (**1**), this conclusion seems justified, for the central group of cells shown in several of his figures is doubtless made up of many embryo initials from which the embryos are elongating. The writer believes that cleavage polyembryony is a very primitive feature, and it is therefore possible that the embryo of *Sciadopitys* is more primitive than that of *Pinus*.

Little is known in regard to the rosette of other conifers. The work done on *Picea* (**28**), *Abies* (**29**), and *Tsuga* (**31**) does not include the stage showing the suspensor elongating. MIYAKE and YAZIN (**30**) have figured a stage in *Pseudolarix* with the suspensor elongated, which proves that a rosette group exists in this genus. It is not safe to conclude that a rosette exists in all forms in which the proembryo is organized in tiers like *Pinus*.

In *Pseudotsuga* LAWSON (**24**) reports a proembryo similar to *Pinus*, but does not show which tier of cells elongates, or whether a rosette exists. He applies the term "rosette" quite generally to the upper tier of free nuclei where no rosette cell group exists. Likewise, COKER, in his work on *Podocarpus* (**6**) and *Taxodium* (**7**), uses the term "rosette" to designate the group of free nuclei above the suspensor. While these investigators apply the term "rosette" here, it is evident from a comparison of the figures that a rosette homologous to that of *Pinus* does not exist in *Podocarpus*, *Taxodium*, or *Cryptomeria*. The term "rosette," as first used by MIRBEL and SPACH (**27**), applies to an unelongated tier of completely walled cells. LAND (**20**) showed that it is likewise the uppermost tier of completely walled cells that elongates in *Thuja*. The absence of a group of rosette cells and of rosette embryos is a more advanced character, found only in the more recent conifers.

SAXTON (**34**) has described the embryo of *Actinostrobus*, which repeats the proembryo of *Sequoia* in completely filling the egg with walled cells. Four of the 6 cells in *Actinostrobus* organize as embryo initials and give rise to embryos. Neither ARNOLDI (**1**) nor LAWSON (**22**), in their work on *Sequoia*, followed the embryo development very far. They probably studied the development of only a single embryo from each egg. It seems probable that the other 3 cells which are cut off by walls in the first 2 divisions of the proembryo of *Sequoia* may represent embryo initials, and more careful study may perhaps reveal secondary embryos arising from 1 or more of these other 3 cells. Like the rosette embryos in *Pinus*, these possible secondary embryos in *Sequoia* may develop only after some delay, and thus easily be overlooked. *Actinostrobus*, and possibly *Sequoia*, represent forms in which cleavage polyembryony has been retained more or less.

The cleavage polyembryony of *Pinus* suggests an explanation of the proembryo of *Ephedra*, described by STRASBURGER (**38**) and LAND (**21**). Here the 8 free nuclei of the proembryo organize with walls as embryo initials, and from 3 to 5 of them produce embryos. The embryo initials organize only at the bottom of the egg in *Pinus*, while in *Ephedra* they organize with walls before reaching the bottom. *Ephedra* has thus retained, in a modified form, a very ancient character, that of cleavage polyembryony, a character which indicates that this plant has descended from the Coniferales. According to the testimony of their embryogeny, such forms as *Pinus* and *Actinostrobus* must be looked upon as the nearest conifer relatives of *Ephedra*.

A comparative study of conifer embryos suggests several possible evolutionary lines of advance. One of these is the one beginning with *Pinus* and culminating in *Ephedra*, in which cleavage polyembryony is retained in some modified form. The apical cell feature is retained among the more primitive embryos of this line, but apparently lost by the time the *Ephedra* level is reached.

The abietineous embryo of the type represented by *Picea* (**38**) would be produced when all the embryo initials together develop 1 embryo. Here the lower tier is an even one, and if the embryo develops uniformly a meristematic group of 4 cells replaces the apical cell from the first. Thus *Picea* may represent the culminating abietineous embryo type, while *Pinus* represents the primitive type.

In his work on *Cephalotaxus* STRASBURGER (**38**) shows in pl. 19, fig. 53, what is possibly a rosette embryo group, although he does not refer to it in the text. It is of interest in this connection to note also that the *Cephalotaxus* embryo has a cap which associates it with *Araucaria* (**4, 38**) and *Agathis* (**12**). All of this suggests another possible line of advance from a *Pinus*-like ancestor, through intermediate forms like *Cephalotaxus*, and a culmination in the embryo of the araucarian type. Thus it looks as though nearly all the embryos of Coniferales may be derived from an ancestor with cleavage polyembryony and an apical cell like *Pinus*, differentiating into the several more or less distinct lines of specialization. This is a strong argument in support of the theory that *Pinus* is a very primitive and ancient genus.

POLYCOTYLEDONY.—If polycotyledonous gymnosperms have been derived from dicotyledonous ancestors, one would expect that in the ontogeny of the cotyledons 2 primordial zones would first appear, and these 2 zones divide up and give rise to the primordia of the separate cotyledons. On the other hand, this investigation goes to prove the opposite; namely, that the polycotyledonous condition is the more primitive, and the tricotyledonous or dicotyledonous condition derived.

Most of the work which has been done on polycotyledony has been based upon the vascular anatomy of the seedling (**16**). The arguments that favor the derivation of polycotyledonous embryos by a splitting of cotyledons are based on anatomy and are well summarized by COULTER and CHAMBERLAIN (**10**), who state that "it must be remembered that these same facts may be used also as evidence that the dicotyledonous condition has arisen from the fusion of more numerous cotyledons."

SAXTON (**33**) also doubts the origin of polycotyledons from dicotyledons, and concludes from a study of cross-sections of *P. pinaster* that "the primordia are exactly equal and equivalent in origin." However, he produced no direct evidence to indicate that fusions of the many cotyledons may have occurred.

The study of the ontogeny of the cotyledons brings out facts not hitherto considered in connection with this problem. In speaking of cotyledonary fusions, it must be understood that full grown cotyledons did not fuse, but 1 cotyledon is developed in the place formerly occupied by 2. The number of cotyledons is actually reduced by fusion of the primordia.

A zygomorphic tendency, which is usually only very slight, is evident in nearly all mature embryos of *P. Banksiana*, but only occasionally in the early stages of the embryo. This zygomorphy of the matured embryo is, no doubt, a secondary result due to the shape of the seed, for it is always oriented within the seed in the same manner, and the zygomorphy is less pronounced in the case of *P. Strobus*, which has a more regularly shaped seed. The zygomorphic tendency found in some early embryos cannot be related to the shape of the seed, and is no doubt due to certain hereditary tendencies. The most extreme case found (text fig. 3*L*) was that of *P. Laricio*. When zygomorphy is pronounced, as in this case, it furnishes an interesting parallel to the development of certain monocotyledonous embryos at the stage when primordia develop, as shown recently by COULTER and LAND (**11**). In *Pinus* the zygomorphy never goes to such an extreme as in the monocotyledonous embryo, and no cotyledonary tube is formed in any of the pines that were studied. That we have well developed cotyledonary tubes among the Abietineae is shown by the work of HILL and DEFRAINE (**16**) and by the recent work of HUTCHINSON (**18**) on *Keteleeria*. The cotyledonary tube would be formed as a natural accompaniment of a coalescence of the many cotyledons by fusion; its very existence among the historically recent gymnosperms is a further indication that cotyledonary fusion has taken place, rather than a splitting. It is interesting to note in this connection that the number of cotyledons in *Keteleeria* is 4, a rather reduced number.

Summary

1. A special technique for dissecting ovules, staining and mounting the embryos, and an improved method of staining embryos in serial sections have been described in detail.

2. The corrosion cavity results from an enzyme, which may be secreted by the unfertilized eggs as well as the embryo.

3. Two forms of polyembryony must be recognized in gymnosperms, namely, cleavage polyembryony and the polyembryony

due to pleurality of archegonia. In *Pinus* one usually finds both types associated in the same ovule, and cleavage polyembryony always occurs in the several species of *Pinus* that were investigated. It is probably a constant feature of this genus.

4. The rosette consists of a group of embryo initials which usually produce embryos. Rosette embryos, like 3 of the 4 primary embryos, are always aborted.

5. Each embryo of a system may be traced back to an initial cell, one of the first completely walled cells of the proembryo. The 8 embryos formed by the cleavage of the egg are therefore definitely organized from the time of the last free nuclear division.

6. A further splitting of one of these 8 embryos into "twins" was not found to occur in *Pinus*. In rare cases 2 matured embryos were found in an ovule, but they were very unequal and due simply to the incomplete dominance of a single embryo.

7. The early embryo develops by means of an apical cell which exists from the time the first walls appear in the proembryo. This apical cell persists for a considerable period, being still recognizable in embryos of 500–700 cells.

8. The apical cell represents a primitive fern character, which is recapitulated in the embryogeny of *Pinus*.

9. Less than 4 primary embryos per archegonium may be produced in case one of the embryo initials, or the early apical cell, disorganizes.

10. The suspensor is formed by the elongation of cells in the basal portion of the embryo, a process that begins with the elongation of the first apical cell segment and continues until the maturity of the embryo.

11. Suspensor cells or embryonal tubes never divide after elongation, but rosette cells may elongate and later divide in forming the rosette embryos, showing their greater potentialities and their distinctness from the suspensor cells which they resemble.

12. Considerable variation occurs in the first secondary suspensor divisions, also in the time of appearance of the first oblique walls formed by the apical cell; both are doubtless related to the time of separation of the embryos.

13. Cleavage polyembryony is a primitive character which *Pinus*, *Sciadopitys*, *Actinostrobus*, and doubtless other genera have

retained. *Ephedra* has also retained it in a modified form, and this definitely associates Gnetales with the Coniferales rather than the cycads.

14. The other evolutionary lines suggested in the discussion likewise assign a primitive position to *Pinus*, so that this ancient type seems to be genetic to several conifer lines.

15. The body regions of the later embryo, so far as they have been determined, appear in the following order: plerome tip of root, periblem and root cap, stem tip, and cotyledons.

16. There is a distinct tendency in *P. Banksiana* toward a reduction in the number of cotyledons, attested by the fact that 2 primordia have been found to form 1 broad cotyledon. This suggests that the dicotyledonous condition has been derived from the polycotyledonous condition through cotyledonary fusions.

17. Cotyledonary tubes are the result of past cotyledonary fusions, and are found in embryos between the primitive polycotyledons and dicotyledons.

18. The zygomorphic feature of a monocotyledonous embryo is foreshadowed in the embryo of *Pinus*.

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DESCRIPTION OF PLATES VI–X

Figures of plate VI from dissected preparations, except figs. 1–5; figures of plate VII all from serial sections; figures of plates VI and VII ×300; figures of plates VIII–X drawn to same scale from dissected preparations and ×80; lettering in all figures as follows: *a*, apical cell; *e*, embryonal tubes; e_1, first embryonal tube (or its initial cell if it marks an unelongated cell); e_2, second embryonal tubes; e_3, third embryonal tubes; *o*, portion of egg containing upper open tier of nuclei; *r*, rosette cells; *s*, suspensor (primary suspensor); *p*, basal plate (plate of thickening usually formed above rosette); all figures of *Pinus Banksiana* unless otherwise indicated.

FIG. 1.—Section through base of archegonium showing suspensor cells (*s*) elongating before lower tier of tip cells (*a*) found in 16-celled proembryo have divided; early corrosion cavity forming; June 20, 1914.

FIGS. 2–5.—Sections through 4 separated embryos all coming from the same egg, still even with each other, but with their apical cell mitosis not simultaneous; mitosis shown results in second embryonal tube initial (e_2); June 20, 1914.

FIG. 6.—Vertical wall forming in second embryonal tube initial, which will result in a 2-celled suspensor division, as shown in fig. 8.

FIG. 7.—Later stage than fig. 6, in which an oblique wall has been formed by apical cell and no vertical wall has yet appeared in any embryonal tube initials.

FIG. 8.—Later stage than fig. 6, in which a 2-celled suspensor division has begun to elongate; first oblique wall cut off by apical cell has just been formed; June 30, 1916.

FIG. 9.—Later stage, in which first oblique wall of apical cell is only slightly tilted; 2-celled embryonal tube division has become well elongated; July 1, 1916.

FIG. 10.—Apical cell of *Pinus Laricio*, forming first oblique wall, in this case almost vertical; July 6, 1916.

FIGS. 11, 12.—Usual appearance of embryos with first oblique wall formed by apical cell; June 29, 1916.

FIGS. 13, 14.—Occasional appearance of embryo after vertical wall has been formed by division as shown in fig. 10; in fig. 14 embryonal tube initials (upper cells of group) have elongated, leaving only 4 cells below; fig. 13, June 22, 1914; fig. 14, July 1, 1916.

FIG. 15.—*Pinus Laricio*, showing how second oblique wall is formed by apical cell after first has appeared vertical; July 16, 1916.

FIG. 16.—Usual condition after first 2 oblique segments have been formed; July 1, 1916.

FIG. 17.—Later stage with distinct apical cell placed slightly to one side; apical cell has 3 cutting faces; June 30, 1916.

FIG. 18.—Usual condition of slightly older embryo; June 29, 1916.

FIGS. 19, 20.—Embryos with apical cell in rather unusual position; June 30, 1916.

FIG. 21.—Two views of same embryo; *a*, in a high plane of focus, showing shadows of lower nuclei; *b*, showing only nuclei of lower plane of focus and walls; apical cell difficult to distinguish with certainty; June 22, 1914.

FIGS. 22, 23.—Older stages than last, with distinct apical cells; July 5, 1916.

FIG. 24.—*Pinus Laricio:* unusual suspensor in which third embryonal tube initial (e_3) remained undivided, although suspensor section above it has 2 collateral tubes; very exceptional; July 6, 1916.

FIGS. 25–27.—Longitudinal sections showing successive stages in development of embryo by apical cell with well marked segments; June 30 and July 5, 1914.

FIG. 28.—Embryo about same stage as fig. 26, but with apical cell placed very much to one side; if section had been cut longitudinally and at right angles to this plane, apical cell would have been obscured; July 5, 1916.

FIG. 29.—Very late stage, in which apical cell is still active and segments very distinct; July 5, 1914.

FIG. 30.—Late stage of embryo with apical cell which has probably become inactive and is on verge of being eliminated; July 5, 1914.

FIG. 31.—Embryo smaller than fig. 29, which no longer possesses an apical cell.

FIG. 32.—Embryo past apical cell stage; July 5, 1914.

FIG. 33.—Two successive cross-sections through the tip of an embryo $100\,\mu \times 180\,\mu$, in which an apical cell may still be found; diagram 33*c* shows relations of segments; July 12, 1916.

FIG. 34.—Three successive cross-sections (*a*, *b*, *c*) through tip of an embryo $128\,\mu \times 280\,\mu$ (larger than any other embryo shown on this plate) in which apical cell may still be found, although doubtless it has become inactive; *d*, section through widest part of same embryo; *e*, segmentation as reconstructed from *a*, *b*, *c;* July 8, 1916.

FIG. 35.—Two successive sections through tip of embryo $108\,\mu \times 200\,\mu$, showing no trace of apical cell.

FIG. 36.—*Pinus Laricio:* drawing of an embryo described (**8**) as coming from splitting of a single embryo on end of a single suspensor cell, showing faint wall of another suspensor cell to right; it is no doubt a case where 2 primary embryos have not completely separated and are sectioned in an unusual position.

FIG. 37.—Two embryo groups of neighboring archegonia in early stage of suspensor formation; apical cell of embryo to left is in mitosis giving rise to first embryonal tube initials; all other embryos have already formed these cells; separation of embryos evident; June 29, 1916.

FIG. 38.—Embryos of same age showing early separation of the 4 primary embryos of each archegonium.

FIGS. 39, 40.—Successive stages in elongation of suspensors, first embryonal tubes, and separation of 4 primary embryos of archegonium; June 26–30, 1916.

FIG. 41.—More complete drawing of later stage with completely separated embryos and partly elongated embryonal tubes; one of the 4 primary embryos has broken loose from its attachment below and enlarged into a balloon at

lower end containing the nucleus; thick deposit of material, basal plate (*p*), is shown on upper wall of rosette; June 24, 1916.

Fig. 42.—Suspensor, of which lower end is beginning to enlarge into a balloon; June 24, 1916.

Fig. 43.—Embryo complex from 2 adjacent archegonia with 8 primary embryos present and 1 set of rosette embryos forming; all first embryonal tubes have elongated and some of second embryonal tubes are about to elongate; June 30, 1916.

Fig. 44.—Embryos from 1 archegonium of about the same stage as fig. 43; 1 embryo has been left far behind in the "struggle for supremacy"; June 22, 1914.

Fig. 45.—Embryo complex similar to fig. 43, but rather more advanced; a balloon-like enlargement may be seen at end of 1 primary suspensor; one of the 8 embryos has been aborted and one left far behind; July 1, 1916.

Fig. 46.—Embryo system from 1 archegonium in which primary suspensors and first embryonal tubes of secondary suspensors have fully elongated, while next divisions of suspensors are nearly half elongated; July 1, 1916.

Fig. 47.—Embryo in which third division of suspensor has completely elongated and succeeding portions of suspensor are beginning to form embryonal tubes of unequal lengths that break joints; suspensor slightly crushed below, thus separating embryonal tubes; July 5, 1916.

Fig. 48.—Embryo slightly older than in fig. 47, but with less developed suspensor becoming massive very suddenly; June 29, 1916.

Fig. 49.—Embryo with very typical suspensor forming fourth suspensor division (third secondary portion), with young embryonal tubes beginning at base; July 5, 1916.

Fig. 50.—Embryo of somewhat older stage than fig. 49.

Fig. 51.—Later massive embryo with characteristic secondary suspensor made up of dovetailed embryonal tubes (or tubes that break joints) in which suspensor divisions no longer appear; July 8, 1916.

Fig. 52.—Older embryo than fig. 51 shortly before differentiation of body regions; July 8, 1916.

Fig. 53.—Rosette in early stage of elongation (cases of elongating rosette cells are found in 5 per cent of embryos of *P. Banksiana*).

Fig. 54.—Rosette fully elongated, with a mitotic figure in lower end of one of its cells; June 30, 1916.

Fig. 55.—Detail of lower end of elongated rosette of fig. 54, showing division spindle.

Fig. 56.—Rosette elongated and divided into embryo of many cells, of which figs. 54 and 55 was a delayed beginning; June 30, 1916.

Fig. 57.—Rosette embryo similar to fig. 56, with suspensor tube broken off from below.

FIG. 58.—Embryo system with first division of rosette embryo showing in one of rosette cells, beginning of usual type of development of rosette embryos; June 27, 1916.

FIGS. 59–61.—Views of rosettes from above, showing stages in development of rosette embryos; June 29–30, 1916.

FIG. 62.—Rosette embryo of *Pinus echinata* in oblique view, showing apical cell; July 23, 1914.

FIG. 63.—Views of rosettes of 2 adjacent archegonia as seen from above, showing different stages in which various rosette embryos may be found at the same time; June 30, 1916.

FIG. 64.—Later rosette embryos well developed, but no tubes elongated to form a suspensor; July 8, 1916.

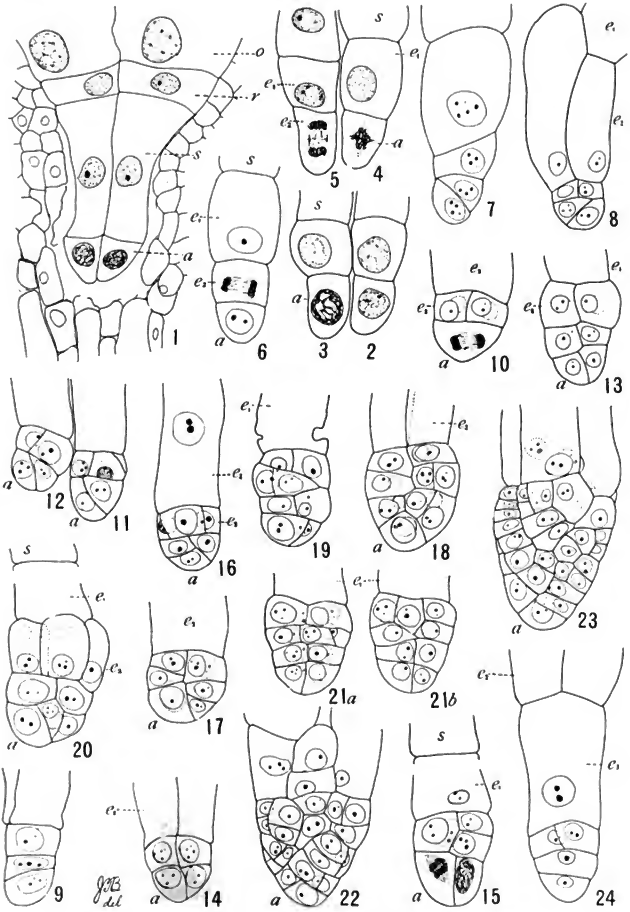
FIG. 65.—Side view of group of rosette embryos, one of which shows an apical cell and distinct segmentation; primary suspensor (*s*) of lower 4 embryos has entirely collapsed by the time this stage is reached; July 8, 1916.

FIG. 66.—Side view of rosette embryos from 2 adjacent archegonia, from some of which embryonal tubes have elongated to form a suspensor, showing that rosette-cell proliferations are real embryos.

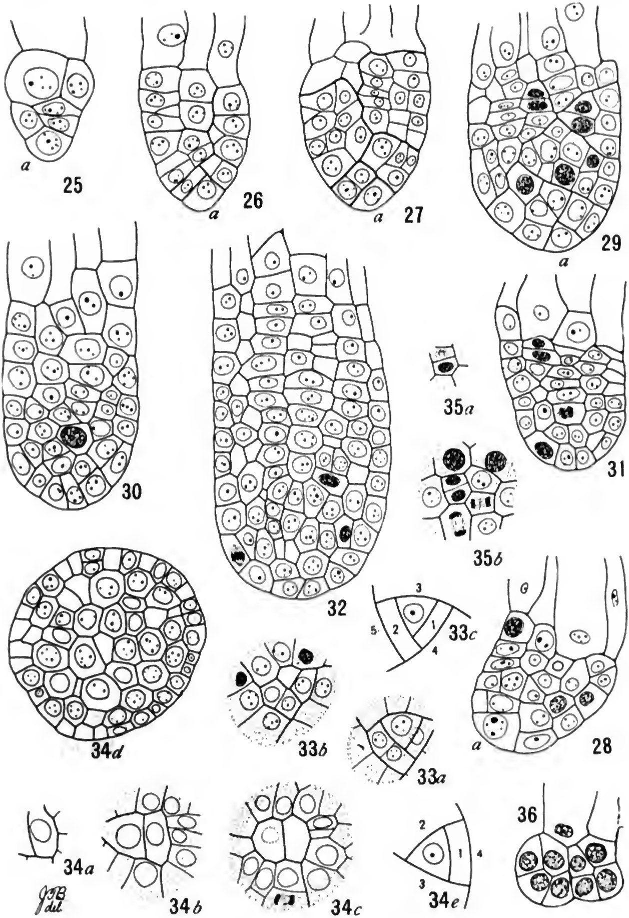
FIG. 67.—Group of rosette embryos which have suspensors elongated in various directions, although number of cells formed is less than in fig. 64, where no elongation has thus far occurred; July 5, 1916.

FIG. 68.—Rosette group showing 1 embryo with suspensor elongating under difficulty and distorted, on account of heavy wall found between rosette and suspensor cells.

FIG. 69.—Embryo system which was badly stunted, due to delay in fertilization or development, while 2 or more adjacent embryo systems gained supremacy; June 29, 1916.



BUCHHOLZ on PINUS



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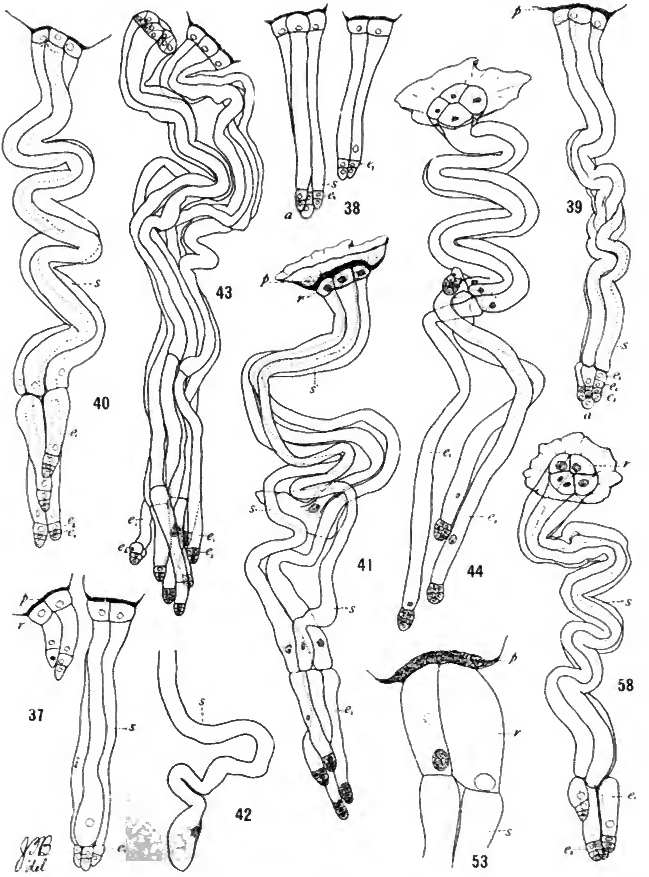

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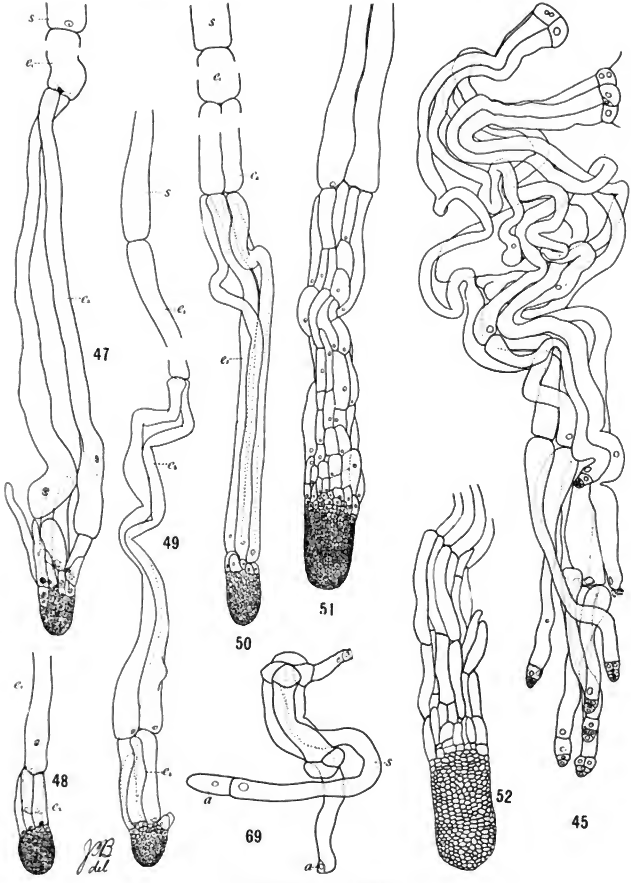
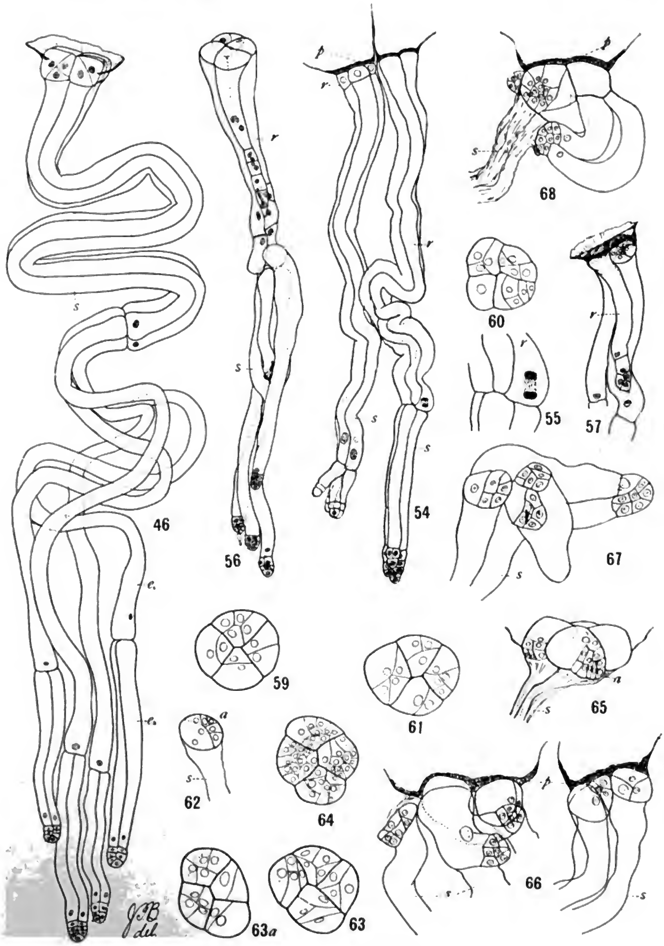


BUCHHOLZ on PINUS



BUCHHOLZ on PINUS

NOTES ON NORTH AMERICAN TREES. II. CARYA

C. S. SARGENT

Conspectus of the species of the United States

Bud-scales valvate, the inner strap-shaped and only occasionally slightly accrescent; fruit more or less broadly winged at the sutures (*Apocarya* C. DC.).

Shell of the nut thin and brittle; leaflets more or less falcate.

Aments of staminate flowers nearly sessile, usually on branches of the previous year; lobes of the seed entire or slightly notched at apex.

Leaflets 13–15; nut ovoid-oblong, cylindrical: seed sweet..1. *C. pecan*

Leaflets 7–11; nut oblong, compressed; seed bitter......2. *C. texana*

Aments of staminate flowers pedunculate, on branches of the year or of the previous year; lobes of the bitter seed deeply 2-lobed.

Leaflets 7–11; nut cylindrical or slightly compressed..3. *C. cordiformis*

Leaflets 7–13; nut compressed, usually conspicuously wrinkled 4. *C. aquatica*

Shell of the ellipsoidal nut thick and hard; lobes of the sweet seed deeply 2-lobed; leaflets 7–9, occasionally 5, rarely slightly falcate; aments of staminate flowers long-pedunculate at the base of branches of the year.................................... 5. *C. myristicaeformis*

Bud-scales imbricated, the inner becoming much enlarged and often highly colored; aments of staminate flowers on peduncles from the base of branches of the year, rarely from the axils of leaves; fruit usually without wings; seed sweet, its lobes deeply 2-lobed (*Eucarya* C. DC.).

Branchlets usually stout, slender in no. 7; involucre 6–12 mm. in thickness, opening freely to the base.

Bark on old trunks separating into long, broad, loosely attached scales; nuts pale.

Branchlets light red-brown; shell of the nut thin.

Leaflets 5 or rarely 7, obovate to ovate, acute or acuminate; nut much compressed, often long-pointed at apex; branchlets glabrous or pubescent......................................6. *C. ovata*

Leaflets 5, lanceolate, acuminate; nut little compressed, acute at apex; branchlets slender, glabrous...7. *C. carolinae-septentrionalis*

Branchlets pale orange color, pubescent; leaflets usually 7–9; shell of the nut thick...................................8. *C. laciniosa*

Bark not scaly, on old trunks dark, deeply ridged; leaflets 7–9, often subcoriaceous, pubescent below; nut reddish brown, often long-pointed, thick-shelled; branchlets pubescent...........9. *C. alba*

Branchlets slender; leaves 5–7-foliolate; involucre of the fruit tardily dehiscent to the middle, indehiscent or opening freely to the base; shell of the nut thick, bark close or sometimes scaly in no. 13.
  Branchlets and leaves not covered when they first appear with rusty brown pubescence.
    Involucre of the fruit 3–5 5 mm. in thickness, opening freely to the base; leaves usually 7-foliolate; winter-buds pubescent.
      Leaflets hoary tomentose below in early spring, slightly pubescent at maturity; petioles and rachis glabrous; fruit broad obovoid; branchlets glabrous.........................10. *C. leiodermis*
      Leaflets covered in early spring with silvery scales, pale and pubescent below during the season; petioles and rachis more or less thickly covered with fascicled hairs; fruit ellipsoidal to obovoid or globose; branchlets glabrous or slightly pubescent.........11. *C. pallida*
    Involucre of the fruit 1–3 mm. in thickness; winter-buds glabrous or puberulous.
      Leaves 5-, rarely 7-foliolate, glabrous or rarely slightly pubescent; fruit obovoid, often narrowed below into a stipitate base, the involucre indehiscent or tardily dehiscent...........12. *C. glabra*
      Leaves generally 7-foliolate, glabrous or rarely pubescent; fruit short-oblong, subglobose or obovoid, the involucre opening freely to the base; bark often more or less scaly................. 13. *C. ovalis*
  Branchlets and leaves densely covered when they first appear with rusty brown pubescence; leaflets usually 5–7; winter-buds rusty pubescent.
    Fruit obovoid; the involucre 2–3 mm. in thickness; peduncles of the aments of staminate flowers often from the axils of leaves; branchlets soon becoming glabrous..........................14. *C. floridana*
    Fruit subglobose to broadly obovoid, ellipsoidal or pyriform, the involucre on the different varieties 2–13 mm. in thickness; branchlets pubescent through their first season................15. *C. Buckleyi*

1. CARYA PECAN Engl. and Graeb.—The pecan was evidently planted by the Indians in the Mississippi Valley, and it is sometimes difficult to determine the natural distribution of this tree. It is probably indigenous in western Mississippi and in West Feliciana Parish, Louisiana, but the statement in my *Silva of North America* that the pecan extended to central Mississippi and Alabama must, I think, be taken to refer to planted or possibly naturalized trees; and it is possible that some of the pecan trees in southern Indiana, especially those toward the Ohio border, were planted by the Indians or are descendants of their trees. Westward in the United States the pecan ranges to the valley of the south fork of the

Arkansas River in Woods County and to Comanche County, Oklahoma, and in Texas to the valley of the Devil's River and to Hardiman County.

2. Carya texana C. DC.—In addition to the stations in Texas and Arkansas (see Trees and Shrubs **2**:206) the bitter pecan has been found near Lake Charles in Calcasieu Parish, and near Laurel Hill, West Feliciana Parish, Louisiana, and near Natchez, Adams County, Mississippi.

3. Carya cordiformis Schn.—This is perhaps the most widely distributed although not the commonest of all the species of *Carya*, as it ranges from southern Maine to the valley of the St. Lawrence River near Montreal and to that of the Ottawa at Hull in the Province of Quebec, and westward to northeastern Nebraska and eastern Oklahoma, and southward to western Florida, northern Alabama, western Mississippi, Louisiana, and eastern Texas. In New England it appears to grow farther north than the other species, but in the valley of the St. Lawrence River in Quebec and Ontario it is associated with *C. ovata*. It grows on the shores of the Straits of Mackinac, Michigan, and in southeastern Minnesota with *C. ovata*, but as it ranges much farther north than that species in Minnesota it must be considered the most northern representative of the genus. In the south Atlantic states from Virginia to southern Georgia it is found from the coast up to altitudes of about 700 m. on the Appalachian Mountains. I have no record of its occurrence in Florida outside the valley of the Apalachicola River or in the coast region of the Gulf states.

To persons who have not read books about trees *C. cordiformis* is generally known, at least in the southern states, as the pignut, and this name should be used for it rather than for *C. glabra* or *C. ovalis* and their varieties, which all have sweet and edible seeds. The first published account of *C. cordiformis* appeared in 1731 in Catesby's *Natural History of Carolina* (**1**:38. *pl. 38*), where it is called "*nux Juglans Carolinensis fructu minims putamiene laevi*, the pignut." Catesby describes the nuts "as not one-quarter part so big as those of the hickory, having both inner and outer shells very thin, so that they may easily be broken with one's fingers. The kernels are sweet, but being small and covered with a very bitter skin, makes them worthless except for squirrels and other wild creatures." CATESBY's figure of a single nut is not a very good one, and at one time led me to suppose that he had figured a nut of some form of *C. ovalis*, but there can be no doubt that his description is that of *C. cordiformis*. In 1770 MUENCHHAUSEN (Hausv. 5:181) called *Juglans alba* of MILLER the pignut among other names. MARSHALL in 1785 described *C. cordiformis* as *Juglans alba minima* and called it the pignut; but in 1787 WANGENHEIM called the *Juglans glabra* of MILLER the pignut and *Juglans cordiformis* the bitternut, and these names appear to have been adopted by all later writers on these trees.

CARYA CORDIFORMIS var. LATIFOLIA Sargent, Trees and Shrubs 2:206. 1913.

New stations for this broad-leaved variety are Fayetteville, Washington County, Arkansas, *E. J. Palmer*, July 15, 1915 (no. 8219), Hannibal, Marion County, Missouri, *J. Davis* (no. 2068), Yellow River and Postville, Allamakee County, Iowa, *O. Schulz*, 1914 (nos. 95 and 30), Toledo, Lucas County, Ohio, *R. E. Horsey*, September 29, 1913.

4. CARYA AQUATICA Nutt.—The water hickory has usually been considered an inhabitant of deep, long inundated river swamps, but toward the southern limits of its range in Florida and Texas it sometimes grows on the high sandy banks of rivers which are only occasionally overflowed, and in dry sandy soil at a considerable distance from streams. The bark of trees in such situations is close, pale, and does not separate into the long, loosely attached scales which are characteristic of this tree when it grows in swamps, although the bark of very old trees growing on dry ground sometimes shows a tendency to flakiness. The trees growing on dry ground have narrower leaflets and usually nuts of a different shape, without the longitudinal wrinkles peculiar to the nut of the water hickory, although some narrower-leaved trees bear nuts of the ordinary size and shape. These southern narrow-leaved trees are so distinct that they may be distinguished as

CARYA AQUATICA var. **australis**, n. var.—Differing from the type in its narrower leaflets, in its smaller ellipsoidal fruit, pale red-brown nuts without longitudinal wrinkles, and in its close pale bark. Leaflets 9–11, lanceolate, acuminate, slightly falcate, minutely glandular-serrate, the terminal raised on a stem 1–1.5 cm. in length, the lateral nearly sessile; when they unfold scurfy-pubescent above and hoary tomentose below, and in the autumn glabrous on the upper surface, pubescent and furnished on the lower surface with small conspicuous tufts of axillary hairs, 6–8 cm. long and 1–1.5 cm. wide. Fruit ellipsoidal, acute at apex, acute or rounded at base, compressed, covered with small scattered yellow scales, 2–2.5 cm. long, about 1 cm. wide and thick; involucre 1–1.5 mm. in thickness, the sutures only slightly winged, tardily dehiscent usually only to the middle; nut oblong to slightly obovoid or semiorbicular, rounded at the ends, compressed, slightly angled, smooth and without longitudinal wrinkles, the shell 1–1.5 mm. thick.

A large tree with close pale bark.

In dry sandy soil in the yard of a house at Alva, Lee County, Florida, *C. S. Sargent*, March 26, 1914, *T. G. Harbison*, September 16, 1914 (no. 2, type). Banks of the Caloosahatchee River near Alma, common, *C. S. Sargent*, March 26, 1916, *T. G. Harbison*, September 16, 1916. Banks of the St. Johns River, Florida, *A. H. Curtiss*, October (no. 2573), no date.

A tree with close bark growing 5 miles west of Jupiter, Palm Beach County, Florida, with leaflets from 1.5 to nearly 2.5 cm. wide (*C. S. Sargent*, March 19, 1914), is probably of this variety, but I have not seen the fruit. A number of trees with pale close bark on the high banks of the St. Johns River at San Mateo, Putnam County, Florida, seen by Mr. HARBISON and me in 1917, in their rather broader leaflets and larger nuts, resembling in shape the nuts of the typical water hickory but without their peculiar wrinkles, seem to connect the variety with the species. I have seen water hickories with close bark and narrow leaflets growing in dry sandy soil near Marshall, Harrison County, Texas, but the fruit of these trees has not been collected.

5. CARYA MYRISTICAEFORMIS Nutt.—The nutmeg hickory connects the two sections *Apocarya* and *Eucarya* of the genus which without this species might well have been considered distinct genera. The valvate bud-scales and the thin involucre of the fruit with prominently winged sutures show its relationship with *Apocarya*, but the thick shell of the nut and the small number of leaflets, 7–9 and occasionally 5, are characters of *Eucarya*. The lobes of the seed are deeply 2-lobed, like those of *Eucarya*, but this is true of two other species of *Apocarya*, *C. cordiformis* and *C. aquatica*. The seeds of these, however, are bitter, while those of

C. myristicaeformis are sweet and edible, like the seeds of *Eucarya*. Nowhere common and very local in distribution, the nutmeg hickory has recently been found on the bluffs of the Yazoo River near Yazoo City, Mississippi, in Richmond Parish in northern Louisiana, at Natchitoches on the Red River in western Louisiana, at Beaumont on the Nueces River in Texas, and at Hugo in Choctaw County, Oklahoma.

6. CARYA OVATA Koch.—The shagbark hickory shows that little reliance can be placed on pubescence as a specific character in this genus, for individual trees have glabrous or pubescent branchlets and glabrous or pubescent leaflets, the two forms often growing together, so that this variation is not dependent on soil or climate, although pubescent individuals are more common in the south than in the north. On some trees the anthers are red and on others yellow. As it is found from the neighborhood of Montreal in the Province of Quebec to southern Minnesota, *C. ovata* grows farther north than the other species of the genus with the exception of *C. cordiformis*. Westward it ranges to southeastern Nebraska eastern Kansas, and eastern Oklahoma. In North and South Carolina it is confined to the Piedmont region, and on the mountains is replaced by *C. ovalis*. In Georgia I have seen it only on Shell Bluff on the Savannah River, below Augusta, near Eatonton, Putnam County, and at Rome, Floyd County. I have no reason to believe that this tree grows in Florida; and from Alabama I have seen specimens only from Valley Head, Dekalb County, and from the neighborhood of Selma, Dallas County, although MOHR credits it to the "Tennessee valley mountain region upper division of the Coast Pine belt." From Mississippi I have seen specimens only from the east central part of the state (Columbus, Starkville, and Brookville), where it is common in its most pubescent form. It has not been found in eastern Louisiana, but it is common in the western part of that state and in southern Arkansas, but is rare in eastern Texas to the valley of the Trinity River. The common form of the fruit is short-oblong to subglobose and depressed at apex, and the nut is then rounded, truncate, or slightly obcordate at apex. The fruit, however, varies considerably in size and shape, and a small-fruited form has been described as var. *Nutallii*

Sargent, Trees and Shrubs **2**:207. 1913. More distinct is a form with oblong fruit and pointed nuts which may be described as

CARYA OVATA var. **ellipsoidalis,** n. var.—Differing from the type in its ellipsoidal fruit and slender branchlets. Fruit bluntly pointed at the ends, much compressed, slightly angled by winged sutures, rough, 3–3.5 cm. long, about 2.5 cm. wide, and 2 cm. thick; involucre opening to the base, 4–5 mm. thick. Nut ovoid to ellipsoidal, abruptly narrowed at apex into a long acuminate point, rounded at base, more or less compressed and prominently ridged.

Missouri, near Hannibal, Marion County, *J. Davis*, September 5, 1913 (no. 2071, type), Oakwood, Rolles County, *J. Davis*, September 13, 1913 (no. 2132). These trees have unusually slender glabrous reddish branchlets for *C. ovata*, but the foliage is of that species, and the white strongly angled nuts, in spite of their abruptly pointed apex, are clearly the nuts of *C. ovata*. To this variety may be referred a tree found by ***James McHugh*** at Indian River, Lewis County, New York, September 15, 1911 (no. 11), which differs from the Missouri trees only in its less compressed fruit with an involucre 5–6 mm. in thickness. Nuts of this species more or less pointed at apex are not uncommon, especially at the north, but I have not seen the ellipsoidal compressed fruit with its comparatively thin involucre of this variety except on the specimens from northeastern Missouri and Indian River, New York.

CARYA OVATA var. **complanata,** n. var.—Differing from the type in its broadly obovoid, much compressed, slightly angled nuts cuneate at base, and rounded truncate or slightly obcordate at apex, and in the oblong-obovoid fruit. Fruit 3 cm. long and about 2.5 cm. wide, with an involucre 5–6 mm. in thickness. Nut 2.2–2.5 cm. in length, 2–2.5 cm. in width, and 1.2–1.4 cm. in thickness, with a shell only 1 mm. thick.

A single tree believed to be 50 years old on the Drushel Farm 2 miles southeast of Mt. Hope in Holmes County, Ohio. For *C. ovata* this tree has unusually slender, sparingly villose branchlets and comparatively small villose buds. The leaves are those of the common form of the species. For the specimens of this tree I am indebted to Professor J. ANDREW DRUSHEL, instructor in nature study and geology in the Harris Teachers' College at St. Louis. In the shape of the nuts this is the most unusual form of *C. ovata* which I have seen, and nuts with such a thin shell are not often found in this species.

CARYA OVATA var. FRAXINIFOLIA Sargent, Trees and Shrubs **2**:207. 1913.—This variety, distinguished by its narrow lanceolate leaflets and the rather thinner involucre of the fruit, was based on specimens collected in western New York. This distinct looking tree is now known to occur in Ohio, Indiana, near Kingston, Ontario, at Keosauqua, Van Buren County, Iowa, and near Myers, Osage County, Oklahoma (*G. W. Stevens*, August 12, 1913, no. 2060).

CARYA OVATA var. **pubescens,** n. var.—Differing from the type in the dense pubescence of pale fascicled hairs on the young branches and on the petioles, rachis, and under surface of the leaflets.

A slight pubescence is not unusual on the branchlets and leaves of *C. ovata*, but this pubescence is sometimes so abundant on individual trees in the southern states that it seems desirable to give them varietal distinction. What I have taken as the type of this variety was collected on May 28, 1918, by *T. G. Harbison* on the bottom lands of the Savannah River at Calhoun Falls, Abbeville County, South Carolina (no. 53). It is a large tree with scaly bark and unusually slender branchlets. The buds are nearly fully grown and are acuminate with the outer scales thickly covered with fascicled hairs. Other specimens referred to this variety are *C. S. Sargent*, banks of Chattanooga Creek, Hamilton County, Tennessee; Valley Head, Dekalb County, Alabama, *T. G. Harbison*, January 26, 1912 (no. 54); *C. Mohr*, Columbus, Lowndes County, Mississippi, October 28, 1898; *T. G. Harbison*, Starkville, Oktibbeha County, and Brookville, Noxubee County, Mississippi, May 3, 1915 (no. 17), October 8, 1915 (nos. 7a, 17a, 26). These trees have slender branchlets and small buds for the species with the exception of those of 17a from Brookville. The pubescence of this tree is rusty brown, but the fruit, which is subglobose and 4 5 cm. in diameter, with an involucre 1 . 2 cm. in thickness, is clearly that of *C. ovata*.

7. CARYA CAROLINAE-SEPTENTRIONALIS Engl. and Graeb.—New stations for this species are Calhoun Falls, Abbeville County, South Carolina, Columbus, Lowndes County, and Brookville, Noxubee County, eastern Mississippi, and the neighborhood of Selma, Dallas County, Alabama.

8. CARYA LACINIOSA Engl. and Graeb.—The range of this species has been extended to southwestern Ontario, to the valley of the Alabama River near Selma, Dallas County, Alabama, and to West Feliciana Parish, Louisiana (*Cocks*).

9. CARYA ALBA Nutt.—Although this species varies in the size and shape of the fruit and nuts, in the thickness of the branchlets, which are densely covered with fascicled hairs when they first appear, and are pubescent or glabrous in their first winter, and in the size of the winter-buds, which are obtuse or acute, it can always

be recognized by the close slightly ridged dark bark which never becomes flaky, by the dense pubescence on the under surface of the leaflets and on the rachis and petioles, and by the conspicuous reticulate veinlets of the leaflets. The fruit varies from globose to short-oblong, obovoid or ovoid, and is rounded or pointed at apex. The involucre is always thick and usually opens freely nearly to the base by 3 or 4 sutures, the valves generally remaining connected below. The nut is more or less compressed, rounded or acute at base, rounded, acute, or acuminate at apex, slightly ridged usually to the base, and tinged with red; in drying the thick shell often cracks transversely.

This is the common hickory of the south Atlantic and eastern Gulf states, and is always called hickory by the inhabitants of that part of the country, descriptive names being used for the other species. It is less common at the north, and I have not seen specimens from any part of New England north of eastern Massachusetts, from eastern Canada, from Ontario except from the southwestern corner, or from New York west of the Hudson River. It is not rare in Ohio, southern Michigan, Indiana, and Illinois, and becomes very abundant in Missouri and Arkansas; in Florida it is rare except in the northern counties. It is one of the commonest species in Alabama, Mississippi, and Louisiana, and reaches eastern Oklahoma and eastern Texas.

The leaflets, which are usually 7, but occasionally 9, vary much in thickness, and a southern form with very large and thick leaflets has been described as var. *subcoriacea* Sargent, Trees and Shrubs **2**: 207. 1913. This is the common form of southern Arkansas and occurs occasionally from Virginia to Florida, through the Gulf states to eastern Texas, and through Arkansas to Missouri, and has been found in Posey County, Indiana (*C. C. Deam*).

A form of *C. alba* with obovoid fruit, narrowed and rounded above and narrowed below into a stipelike base and compressed nuts acuminate at the ends, has been described as var. *ficoides* Sargent (*l.c.* 206). The type of this variety is in a cemetery at Webb City, Jasper County, Missouri. The same form was collected in 1894 at Ocean Springs, Jackson County, Mississippi, by Josehine Skehan. Nuts of *C. alba* acute or acuminate at apex are not rare, and trees producing such nuts occur in eastern Pennsylvania and are generally distributed through the southern states. Such pointed nuts are usually acute or acuminate at base and are inclosed in involucres which are oblong, gradually narrowed and rounded at base, and acute or acuminate at apex; but a tree at Noel, Missouri, produces ovoid fruit broad and rounded at base and gradually narrowed and rounded at apex, which is so different from that of other forms of this species which I have seen that it may be distinguished as

CARYA ALBA var. **ovoidea,** n. var.—Differing from the type in its ovoid fruit with a thinner tardily dehiscent involucre. Leaves small for the species, not more than 20 cm. long, with densely pubescent petioles and rachis, and 7 thin leaflets. Fruit smooth and lustrous, not at all compressed, 3.5–4.5 cm. long and 2.5–3 cm. in diameter; involucre not more than 4 mm. in thickness, remaining entirely closed or opening tardily by 2 or 3 of the sutures nearly to the middle. Nut rounded at base, gradually narrowed into a long acuminate apex, irregularly ridged to below the middle, much compressed.

A tree 15 m. high with rough ridged gray bark.

Noel, McDonald County, Missouri, *E. J. Palmer*, September 5, 1913 (no. 4119, fruit, type), October 23, 1910 (no. 3287, leaves).

On the grounds of the P. J. Berckmans Nursery Company, a few miles west of Augusta, Georgia, there is a hickory tree which bears the large oblong acute fruit and acuminate nuts rounded at base of one of those extreme forms of *C. alba* which produce pointed nuts. The bark of this tree is indistinguishable from that of a tree of *C. alba* which is growing close to it. It has glabrous branchlets, however, as slender as those of *C. ovalis*, and acute pubescent terminal winter-buds 8–10 mm. long. The leaves are 7-foliate with thin leaflets and are only slightly pubescent. *C. pallida* grows near this tree, and there are individuals of *C. glabra* not far off. I should have suspected that this tree might be a hybrid between *C. alba* and one of these species, but I can find no trace of either of them in the fruit which is distinctly that of *C. alba*. It may be described as

CARYA ALBA var. **anomala,** n. var.—Differing from the type in its nearly glabrous leaves with smaller leaflets, in its slender glabrous branchlets, and in its smaller winter-buds. Leaves 7-foliate; petioles and rachis only slightly pubescent; leaflets thin, acuminate, finely and remotely dentate, puberulous below and pubescent on the lower side of the midribs, 14–20 cm. long and 4–6 cm. wide. Fruit oblong, rounded at base, acute at apex, 5 cm. in length; involucre 6 mm. in thickness; nut oblong, rounded at base, acute at apex, compressed, slightly angled to the middle or nearly to the base.

A tree with bark indistinguishable from that of *C. alba* with which it is growing, slender red-brown lustrous glabrous branchlets and acute pubescent terminal buds only 8–10 mm. in length. A single tree on the grounds of the P. J. Berckmans Nursery Company, a few miles west of Augusta, Georgia. This is one of the most abnormal hickory trees I have seen. Without the fruit it might easily be taken for one of the forms of *C. ovalis*, but the fruit and the nuts are clearly those of *C. alba*.

10. **Carya leiodermis,** n. sp.—Leaves 7-, rarely 5-foliolate, 30–35 cm. long with slender petioles and rachis slightly or densely pubescent with fascicled hairs, becoming glabrous or nearly glabrous; leaflets thin, finely serrate, long-pointed at apex, gradually narrowed, cuneate and unsymmetrical at base, the terminal oblong-obovate, raised on a slender pubescent petiolule 1–1.5 cm. in length or nearly sessile, of the same shape and often smaller than those of the upper pair of nearly sessile lateral leaflets; leaflets of the lower pairs lanceolate, petiolulate, much smaller; when they unfold densely covered on the lower surface with hoary tomentum, pubescent above and often ciliate on the margins; fully grown in April when the flowers open, and at maturity dark green and lustrous on the upper surface, pale and slightly pubescent on the lower surface, those of the upper pair 12–15 cm. long and 5–6 cm. wide, with stout midribs more or less densely pubescent on the lower side. Aments of staminate flowers 10–12 cm. long, on slender puberulous peduncles, their bracts lanceolate, puberulous; bracts of the flower ovate, lanceolate, furnished on the margins with long white hairs mixed with stipitate glands, one-third longer than the ciliate calyx lobes; anthers red, covered with long white rigid hairs. Pistillate flowers in short spikes, their involucres and bracts densely clothed with long white hairs. Fruit broadly obovoid, smooth, glabrous or slightly pubescent, sparingly covered with small white scales, 4–4.5 cm. long and 3.5–4 cm. in diameter; involucre 5–5.5 mm. in thickness, opening freely to the base usually by 2 sutures only;

nut oval to slightly obovoid, rounded at the ends, tinged with red, about 3 cm. long and broad and 2.5 cm. thick; shell 4–5 mm. in thickness; seed small and sweet.

A tree 20–25 m. high, with a trunk sometimes 50 cm. in diameter, covered with close only slightly ridged pale bark, and slender reddish brown lustrous branchlets puberulous or pubescent when they first appear, becoming glabrous or almost glabrous by the end of their first season. Terminal winter-buds acute, about 1 cm. long, the outer scales pubescent, the inner covered with appressed pale hairs and ciliate on the margins; axillary buds ovate and rounded at the apex or subglobose.

LOUISIANA: Low woods on Little Bayou Têche 4 miles east of Opelousas, Caddo Parish, *R. S. Cocks* and *C. S. Sargent*, October 11, 1913 (no. 5, type), *R. S. Cocks*, April 1914 (nos. 5, 9, 13, 14); Lake Charles, Calcasieu Parish, *C. S. Sargent*, March 23, 1917; Natchitoches, Natchitoches Parish, *R. S. Cocks*, September 1914 (no. 17), *E. J. Palmer*, April 27, 1915; Grand Ecore, Natchitoches Parish, *E. J. Palmer*, April 28, May 5, 1915 (nos. 7411, 7412, 7524), April 15, 1916 (no. 9452); dry woods, Winnfield, Winn Parish, *Cocks* and *Sargent*, April 6, 1913; Tangipahoa Parish, *Cocks* and *Sargent*, March 28, 1917, roadside between Springfield and Ponchatoula, *Sargent* and *Cocks*, March 29, 1917, Loranger, *Sargent* and *Cocks*, March 30, 1917.

ARKANSAS: Fulton, Hempstead County, *E. J. Palmer*, October 18, 1915 (no. 8953).

MISSISSIPPI: Bluffs, Yazoo City, Yazoo County, *T. G. Harbison*, May 1 and 30, 1915 (nos. 22, 36, 37), October 26 and 28, 1916 (nos. 46, 48).

The slender often glabrous branchlets of *C. leiodermis* show its relationship with *C. ovalis;* the close bark, the thick involucre of the fruit, the reddish nut, and the pale tomentum on the under surface of the young leaflets indicate a connection with *C. alba*, and its proper position seems to be between these two species.

CARYA LEIODERMIS, var. **callicoma,** n. var.—Differing from the type in the thinner involucre of the fruit and in the bright red color of the unfolding leaves. Leaves 7-foliate, the young leaflets coated below with hoary tomentum, ciliate on the margins and scurfy-pubescent above, bright red and very fragrant, and at maturity thin, dark green and lustrous on the upper surface and yellow-green and nearly glabrous on the lower surface. Fruit slightly obovoid, smooth, nearly glabrous, usually 3–3.5 cm. long or rarely not more than 2 cm. long; involucre 2.5–3 mm. in thickness, opening tardily nearly to the base by 2 or 3 sutures; nut rounded at the ends, compressed, only slightly angled, pale brown, 1.5–2.5 cm. long and wide, the shell 3.5 mm. in thickness.

A tree 25–30 m. in height, with a tall trunk sometimes 1 m. in diameter, covered with close gray-brown ridged but not scaly bark, ascending and spreading branches forming a narrow round-topped head, and slender glabrous red-brown branchlets marked by numerous pale lenticels.

LOUISIANA: Low woods, borders of streams and river banks often overflowed; Lake Charles, Calcasieu Parish, *C. S. Sargent*, April 2 and 3, 1913, April 12, 1914, *R. S. Cocks*, October 1913, September 1914, *R. S. Cocks* and *C. S. Sargent*, April 12, 1915; West Lake Charles, *R. S. Cocks* and *C. S. Sargent*, April 1913.

TEXAS: Low woods near Beaumont, *C. S. Sargent*, April 11, 1915, *E. J. Palmer*, April 22 and September 11, 1916 (nos. 9528, 9532, 10694, 10695).

MISSISSIPPI: Vicksburg, Warren County, *T. G. Harbison*, October 28, 1916 (no. 3); near Natchez, Adams County, *Miss C. C. Compton*, May 1915; Jackson, Hinds County, *T. G. Harbison*, April 29, 1915; Taylor, Lafayette County, *T. G. Harbison*, April 14, 1915 (no. 7); Rockport, Copiah County, *T. G. Harbison*, 1915, 1916, 1917 (nos. 2, 3, 15, 16, 17); Columbus, Lowndes County, *C. S. Sargent*, October 12, 1914; Starkville, Oktibbeha County, *T. G. Harbison*, April and October, 1913 (nos. 1059, 1283).

From other hickories this variety differs in the bright red color of the young foliage, which in early spring makes it one of the most distinct and beautiful trees in the forests in the neighborhood of Lake Charles, where it is common. It may be expected to occur generally in the region between Lake Charles and the valley of the lower Nueces River, Texas.

11. **Carya pallida,** nov. comb.—*Hicoria pallida* Ashe, Notes on hickories. 1896.—This tree is closely related to *Carya ovalis* Sargent, but may be distinguished from all the forms of that species by the pale under surface of the leaflets, by the silvery scales on the young foliage, and by the prominent and persistent clusters of fascicled hairs on the petiole, rachis, and under side of the midrib. The leaves are 7-, rarely 9-foliate, and vary from 1.5 to 6 cm. in width. The fruit is pubescent and varies from ellipsoidal to obovoid or to broad-obovoid and to subglobose or depressed globose, and from 2 to 4 cm. in length, and is not easily distinguishable from that of some forms of *C. ovalis*. The involucre varies from 3 to 4 mm. in thickness and splits tardily to the base, usually by 2 or 3 of the sutures. The nut is white, rounded at the ends or occasionally slightly obcordate or obtusely pointed at apex, compressed and more or less prominently ridged nearly to the base. On a tree growing on the grounds of the Country Club at Summerville, near Augusta, Georgia, the fruits are pyriform, 5 cm. long, and contracted below into a stipelike base with an involucre 5 mm.

thick and oblong much compressed nuts narrowed at apex. The branchlets of *C. pallida* are slender, glabrous or pubescent, and the winter-buds are acute or obtuse, and are covered with yellow scales. When *C. pallida* grows in rich soil it sometimes attains a height of 30–35 m. and forms a trunk 6 m. in diameter. On such trees the bark is pale and only slightly furrowed. On dry stony ridges trees more than 10–15 m. tall are not common, and the bark of trees growing in such soil is sometimes nearly black, very rough with prominent ridges.

Carya pallida grows in New Jersey in sandy soil in the neighborhood of Cape May. It is common in sandy soil in southern Delaware and in the southern part of the Maryland peninsula. It is common in Gloucester and James City counties, Virginia, where it often grows in rich soil and attains its largest size. It occurs in Isle of Wight County, Virginia, and is common in the Piedmont region of North and South Carolina, and in the western parts of these states ascends into mountain valleys up to elevations of 700 m. above the sea-level. It is common in northern and central Georgia, and occasionally reaches the Georgia coast. It grows at Bainbridge, southwestern Georgia, and in Leon and Gadsden counties, Florida. In Alabama it is the common hickory on the dry gravelly and poor soil of the upland table lands and ridges of the central part of the states, and extends into the southwestern counties. The western stations from which I have seen specimens of this tree are Chattanooga, Tennessee, Yazoo City, Mississippi, where it is common on the bluffs of the Yazoo River, and northeastern Louisiana (near Kentwood, Tangipahoa Parish, *Cocks*).

Trees of this hickory can easily be recognized at a distance by the pale color of the under surface of the leaves, and southward by the dark, deeply fissured bark of the trunk, which is not found on other hickories in the southeastern states. Formerly I considered that *C. pallida* was the same as *C. villosa* from Allenton, Missouri, and other authors have adopted this view, but further observations show that it can be distinguished from that tree by the absence of the rusty brown pubescence from the unfolding leaves and young branchlets, by the silvery scales on the young leaves, by the pale color of the under surface of the leaflets, and by the thicker involucre of the larger often ellipsoidal or globose fruit.

12. CARYA GLABRA Sweet.—The name pignut, which should be confined to *Carya cordiformis*, has been generally applied to many trees with smooth or slightly scaly bark, slender branchlets, small winter-buds, and pear-shaped or globose fruit. The husk of the fruit of these trees varies in thickness; it remains closed or opens

only at the apex or splits to the base; it is puberulous and, like the involucre of the pistillate flower, is covered more or less thickly with yellow scales, which are usually found also on the lower surface of the 5 or more commonly 7 leaflets. The different forms of these trees intergrade, and it would be possible to consider them forms of one species; but as the trees with close bark usually produce pear-shaped fruits which remain closed or open tardily to the middle, and generally by only 1 or 2 sutures, and as the trees with scaly bark bear fruit which, although round or pear-shaped on different forms, always splits freely to the base, it seems convenient to group these different forms under two species, chiefly distinguished by the indehiscent or dehiscent involucre of the fruit. The earliest post-Linnaean name for any of these trees is *Juglans glabra* of MILLER, published in the eighth edition of his *Dictionary* in 1768. MILLER'S species is based on CLAYTON'S *Juglans alba fructu minori, cortice glabro.* Trees with close bark and indehiscent pear-shaped fruit and trees with slightly scaly bark and globose dehiscent fruit are common in Gloucester County, Virginia, where CLAYTON lived for many years and where he probably made most of his observations on trees, but the "cortice glabro" seems to point to the tree with close bark and pear-shaped indehiscent fruit. If this view is correct and the trees with indehiscent fruit are treated as representatives of a distinct species, this becomes

Carya glabra Sweet, Hort. Brit. 97. 1827; Torrey, Fl. N.Y. **2**:182 (in part). *pl. 101.*

Juglans glabra Miller, Dict. ed. 8, no. 5. 1768.

Juglans porcina Michaux f., Hist. Arb. Am. Sept. **1**:206 (in part). *pl. 38. figs. 1, 2.* 1910.

Carya porcina Nuttall, Gen. **2**:222 (in part); Sargent, Trees and Shrubs **2**:199. *pl. 179.* 1913.

The fruit of this tree is obovoid, compressed, rounded at apex, gradually narrowed below and often abruptly contracted into a short stipelike base; the involucre is 1.5–2.5 mm. in thickness and opens tardily generally by 1 or 2 sutures, or often remains closed. The nut is compressed, obovoid, slightly obcordate or acute at apex, gradually narrowed at base, not ridged, and light colored with a hard thick shell and small sweet seed. The leaves are usually 5-, rarely 7-foliolate, and more or less thickly covered with yellow scales. The bark is close and shows no tendency to become flaky. This is one of the least common of the forms of the so-called pignut, but ranges from southwestern Vermont to western New York and southeastern Ontario (Queensland Heights), and southward to Delaware, the District of Columbia, eastern Virginia, and along the Appalachian Mountains to North Carolina; it occurs in northern, central, and eastern Georgia, northern Alabama, eastern Mississippi, and in southern Indiana, where it is common, and in southeastern Illinois (*H. A. Gleason* in Herb. Gray). MICHAUX's figure on which SWEET based his *Carya glabra* represents a rather longer fruit than that of the common form of this tree and the involucre has opened by 4 sutures nearly to the middle of the fruit. *Carya glabra* passes into

CARYA GLABRA var. **megacarpa,** nov. comb.—*Carya megacarpa* Sargent, Trees and Shrubs **2**:201. *pl. 180.* 1913; *Carya ovalis* var. *megacarpa* Ashe, Torreya **18**:74. 1918.—Differing from the type in its larger fruit with a thicker involucre and in its usually stouter branchlets and larger winter-buds.

This tree has larger fruit with a thicker involucre, usually stouter branches, larger buds, and close bark which shows little tendency to become flaky. The thickness of the branchlets, the size of the buds, and the size of the fruit, however, cannot always be depended upon to distinguish this form, for some of the southern trees which bear the largest fruit have branchlets as slender as the northern small-fruited trees; and trees with stout branchlets sometimes produce as small nuts as the small-fruited form of *C. glabra*. This variety is usually glabrous, but on a tree in Rochester, New York, and on one at Brunswick, Georgia, the leaves are distinctly pubescent. The fruit varies from 2.5 to 4.5 cm. in length, with an involucre 2.5–3 mm. in thickness and is occasionally entirely covered with bright yellow scales; it varies from oblong-obovate, with a distinctly stipelike base, to short-obovate and rounded at base, or to subglobose. The nut is rounded or acute at the ends. The leaves are 5–7-foliate.

In the north this form has been seen only near Rochester, New York, on the New Jersey Coast, in the District of Columbia, and in southern Illinois; it is one of the most abundant hickories in the coast region of the southeastern states from North Carolina to the Florida peninsula, and to Alabama, where it is a common tree on the shores of Mobile Bay, and Louisiana. It ranges occasionally inland to central and northern Georgia and to western Mississippi.

CARYA GLABRA var. MEGACARPA f. **angulata,** n. f.—Differing from the type in the striately angled nuts. The fruit of this form is broadly obovoid, depressed at apex, 2.5–3 cm. long, 2.8–3 cm. wide, and about 2.5 cm. thick; the involucre is 3–4 mm. in thickness and remains closed after the fruit is perfectly dry. The nut is subglobose, but rather broader than high, and conspicuously angled to the base, with a shell 4–5 mm. in thickness. The leaves of this form are 5–7, usually 7-foliolate. It is a tree with wide spreading branches, pale gray shallowly grooved close bark, slender glabrous bright red-brown lustrous branchlets, and acute winter-buds, the terminal 5–8 mm. long, their outer scales covered with gray pubescence.

Borders of salt marshes, near Brunswick, Glynn County, Georgia, *T. G. Harbison*, March 26 and October 1, 1913, November 13, 1914 (nos. 1024 type, 1025, 1027, 1028).

13. CARYA OVALIS (Wangenheim) Sargent, Trees and Shrubs **2**:207. 1913.—This is the oldest name which can be used for the small-fruited hickories with globose or pear-shaped fruit opening usually as soon as ripe to the base generally by the 4 sutures of the thin involucre, and often with slightly scaly bark. The type of this tree and its varieties have glabrous or rarely slightly pubescent leaves, with usually 7 thin leaflets. The type of the species, judging by WANGENHEIM's figure, has short-oblong fruit rounded at base, acute at apex, 2.5–3 cm. long and about 1.5 cm. in diameter, with an involucre 2–2.5 mm. in thickness. This is one of the least common of the forms of this tree, and occurs from western New York and eastern Pennsylvania to Illinois, and southward to the mountains of North Carolina and Tennessee, and to central Georgia and Alabama. The following varieties can be distinguished:

CARYA OVALIS var. OBCORDATA Sargent, *l.c.* 208. 1913, with subglobose to short-oblong fruit 2–3 cm. in diameter. The bark often separates into narrow scales, but on some trees shows no tendency to become scaly.

This is the commonest and the most widely distributed of the northern forms of this tree and the *Carya* or *Hicoria microcarpa* of many recent authors. It is common in southern New England and ranges to Wisconsin, southwestern Missouri, western North Carolina, central and eastern Georgia, eastern Mississippi, and to central Alabama, where it is very common in the mountain districts. On the Carolina mountains this tree grows to a large size and is sometimes called scaly-barked hickory. On dry ridges in Macon County, North Carolina, and near Birmingham, Alabama, the bark is close and darker, and some of the trees look distinct from the red color of the petioles which they retain during the season.

CARYA OVALIS var. OBCORDATA, f. **vestita,** n. f.—Differing from the var. *obcordata* in the thick tomentose covering of the branchlets during their first year. The leaflets of this form are slightly pubescent in the autumn on the under surface of the midribs. Although the nuts are more compressed than those of the ordinary forms of var. *obcordata*, the fruit is of that variety. The branchlets are unusually stout for a form of *C. ovalis* and are covered with rusty tomentum during their first year and are more or less pubescent in their second and third seasons.

A large tree on the low border of Davis Pond 14.3 miles southwest of Decker, Knox County, Indiana, *C. C. Deam*, October 5, 1917 (no. 24, 144 type).

CARYA OVALIS var. ODORATA Sargent, *l.c.* 1913.—The fruit of this form shows less tendency to vary than that of the other forms and is subglobose or slightly longer than broad, much flattened and 1.3–1.5 cm. in diameter, with an involucre often not more than 1 mm. thick. The bark of old trees is often scaly.

This form is not common, but ranges from southern New England, eastern Pennsylvania, and the District of Columbia to western New York, Ohio, Indiana, southeastern Ontario, and southern Illinois. From the southern states I have seen specimens only from the neighborhood of Atlanta, Georgia, and from Starkville, Oktibbeha County, Missisisppi.

CARYA OVALIS var. BOREALIS Sargent, *l.c.* 1913.—This variety differs from *C. ovalis* in its pubescent branchlets and winter-buds and in the pubescence on the leaves early in the season. It has ellipsoidal or ovoid flattened fruit with an involucre 3–3.5 mm. thick and an ovoid nut conspicuously ridged to the base. The bark is scaly.

This variety has only been noticed in southwestern Michigan.

CARYA OVALIS var. OBOVALIS Sargent, *l.c.* 1913.—This form has more or less obovoid fruit about 2.5 cm. long and 2 cm. in diameter. The fruit resembles in shape that of *Carya glabra*, but the involucre is thicker and splits easily to the base or nearly to the base.

This form is found from southern New England to Missouri and northern Arkansas, and occurs on the mountains of North Carolina, on the coast of Georgia, and in northern central Alabama, and is the common "pignut" in the middle western states.

CARYA OVALIS var. OBOVALIS f. **acuta,** nov. f.—*Carya porcina* var. *acuta* Sargent, Trees and Shrubs **2**:200. *pl. 179. figs. 9, 10.* 1913.—In spite of its close bark this tree seems to belong with *C. ovalis* rather than with *C. glabra*. The bark and the nuts pointed at the ends afford the only characters by which it can be distinguished from *C. ovalis* var. *obovalis*.

CARYA OVALIS var. **hirsuta,** nov. comb.—*Hicoria glabra hirsuta* Ashe, Notes on hickories. 1896.—This is a common tree on the southern Appalachian Mountains of North Carolina at elevations of from 1200–1500 m. above the sea, and occasionally grows to a height of 20–25 m. with a trunk diameter of 6 m. The scaly bark of this tree shows its relationship with *Carya ovalis* rather than with *C. glabra*, and I have taken up ASHE's name, although the petioles and lower surface of the leaflets are not tomentose as he describes them, but pubescent, the fascicled hairs which are more or less abundant on different individuals being most numerous on the under side of the midribs. The fruit is pyriform, usually narrowed below into a short stipitate base, 3–4.5 cm. in length, more or less compressed, with an involucre tardily dehiscent, usually opening only to the middle, and 1.5–3 mm. in thickness. The nut is compressed, very slightly ridged, and rounded at the ends, with a thin shell and a sweet seed. The winter-buds are pubescent, acute or obtuse, the terminal varying from 7 to 14 mm. in length.

Highlands, Macon County, North Carolina, *T. G. Harbison*, 1913 and 1914 (no. 1). *Harbison* no. 1250, June and October 1914, with less pubescence and slightly obovoid fruit, with a thin involucre splitting freely to the base and a slightly obovoid nut, appears to be a form connecting the variety with the species.

14. CARYA FLORIDANA Sargent, Trees and Shrubs **2**:193. *pl. 177.* 1913.—When I described this species I had not seen terminal winter-buds and I mistook it for an *Apocarya*. Collections made later show that the terminal winter-buds are ovate, acute or obtuse, and 5–7 mm. long, and that the scales are imbricated and covered with close rusty pubescence and more or less thickly with yellow or rarely silvery scales. The branchlets are glabrous or pubescent during their first winter. Later collections show that the fruit is obovoid, gradually narrowed, rounded, and sometimes slightly

depressed at apex, narrowed below into a short stipelike base, occasionally slightly winged at the sutures, sometimes roughened by prominent reticulate ridges, puberulous and covered with small yellow scales, 2–3.5 cm. long and 2–2.5 cm. in diameter; the involucre is 2–3 mm. in thickness, splitting to the base by usually 2 or 3 sutures. The nut is pale or reddish, subglobose, and not more than 1.5 cm. in diameter, or ovate, acute at base, narrowed and rounded at apex, slightly compressed, or rarely oblong and acute at base, rounded at apex, and 2.5–3 cm. long and 2 cm. wide; the shell varies from 2–3 mm. in thickness; the cotyledons are sweet.

Although the fruit and thin branchlets of *C. floridana* resemble those of the *glabra-ovoidea* group, the thick rusty pubescence on the young leaves and branchlets separates it from all the plants of this group. It differs from them also and from other hickories in the occasional appearance of the aments of staminate flowers from the axils of leaves, and in the fact that it is often shrubby in habit and produces large crops of fruit on stems not more than 2–3 m. high. The sessile, or nearly sessile, terminal leaflet is also unusual in the genus.

Carya floridana is common on the eastern coast of Florida, growing on dry sandy ridges and low hills from Valusia County southward to Jupiter Island, Palm Beach County. It is common, too, usually as a small shrub near Orlando in Orange County and southward to De Soto County, and occurs on the shore of Pensacola Bay.

THE TEXAS HICKORY.—In 1860 BUCKLEY described his *Carya texana* in Proc. Philad. Acad. As the name was otherwise occupied DURAND changed it to *C. Buckleyi*, and as BUCKLEY described the fruit as globose with a thin involucre *C. Buckleyi* has been adopted for a tree with globose fruit, a thin involucre, and pale red nearly globose nuts. This tree with the round nuts is common in the neighborhood of Denison, Grayson County; it grows also near Jacksonville in Cherokee County, at San Augustine, San Augustine County, and at North Pleasanton, Atascosa County, and in Oklahoma on dry sandy hills west of Muskogee, Muskogee County.

The hickory with obovoid or ovoid fruit, often with an involucre varying greatly in thickness, and with an oblong or slightly obovoid compressed slightly angled pale nut, which I described as *C. arkansana* (Trees and Shrubs **2**:203. *pl. 181*), is much more common and more widely distributed in Texas, and it is probable that BUCKLEY had the 2 trees in mind when he described his *C. texana*, for when they grow together in dry sterile soil, as in the neighborhood of Denison, they both have thick nearly black fissured bark and cannot be distinguished except by the shape of the fruit. Farther north and in better soil the bark of *C. arkansana* is thinner, lighter-colored, and is inclined to separate into small thin scales. The unfolding leaves and the young branchlets of both trees are thickly covered with tawny pubescence mixed on the under side of the leaflets with small silvery scales. This pubescence distinguishes them and *C. floridana* from all the other species of the United States. The size and shape of the fruit and the thickness of the involucre do not afford good specific characters in *Carya*, and the nature of the bark is so dependent within certain limits on the soil in which the individual grows that this cannot be depended upon for distinguishing species. The winter-buds on both trees are covered with brownish pubescence in which silvery scales are more or less scattered; and the long white hairs found at the apex of the scales of the former sometimes occur but are perhaps more often wanting from the scales of the latter. The thick tawny pubescence is the most distinct and constant character of all the forms of this tree. The form with obovoid fruit can perhaps best be treated as a variety which becomes

15. CARYA BUCKLEYI var. **arkansana,** nov. var.—*C. arkansana* Sargent, Trees and Shrubs **2**:203. *pl. 181.* 1913.—Differing from the type in the obovoid to ellipsoidal or ovoid fruit with a usually thicker involucre, and in the oblong more compressed pale-colored nuts.

The type region of this tree is the valley of the Arkansas River at Van Buren, near Fort Smith, in the extreme western part of the state of Arkansas. It has been found growing in sandy soil near Vollmer, Knox County, Indiana (*C. C. Deam*, no. 18232, August 28, 1915), and it is common in northeastern Missouri, where it has been collected by the Reverend JOHN DAVIS at a number of stations near Hannibal. It is the common hickory on the Ozark Mountains in northwestern Arkansas, where it is very abundant on dry rocky ridges at elevations of 400–600 m., and occurs in several other parts of Missouri and in Arkansas and eastern Oklahoma. It is not rare in western Louisiana, where it has been collected in the neighborhood of Opelousas, at Winnfield, and near Alexandria. In Texas it is the common hickory from the coast to the base of the Edwards Plateau and as far south as the valley of the Atascosa River in Atascosa County, where it was first collected by BUCKLEY in June 1881. From farther northwest I have seen specimens only from Fredericksburg in Gillespie County. As in other species of the genus, there is considerable variation in different individuals. The fruit is obovoid, rounded or gradually narrowed at the base or abruptly contracted into a more or less developed stipe, or ellipsoidal or ovoid and rounded at the ends; it varies from 2 cm. to 5 cm. in length and in diameter. The involucre varies from 2 mm. to 4 mm. in thickness, the largest fruit with the thickest involucre being found in southern Arkansas and western Louisiana, and the smallest in northern Missouri. The nuts are oblong to slightly obovoid, compressed and rounded at the ends and vary much in size but little in shape or in the thickness of the shell, which is unusually thick for a species of this group. The thickness of the branchlets, which are pubescent during the first year, and the size of the winter-buds vary on different trees. The leaflets as they unfold are covered above by small scattered yellow scales and on the lower surface are thickly clothed with thicker tawny scales mixed with silvery white scales, and are pubescent on the midribs and veins, traces of these fascicled hairs being persistent during the season. The scales and fascicled hairs are also found on the young petioles and rachis, which usually become quite glabrous before the end of the season. The yellow scales, sometimes mixed with short hairs, are more or less persistent on the fruit and on the winter-buds.

CARYA BUCKLEYI var. ARKANSANA, f. **pachylemma,** n. f.—Differing from the var. *arkansana* in its larger fruit with a thicker involucre. The fruit of this form is 5–6 cm. long and 4–5 cm. in diameter with an involucre 1.2–1.3 cm. in thickness; the nut is rounded at the ends, slightly angled, compressed, from 3.2 to 3.5 cm. long and about 3 cm. wide.

A large tree with thick deeply fissured pale gray bark, small drooping unusually slender nearly glabrous branchlets and rusty pubescent winter-buds.

Rich woods, Fulton, Hempstead County, Arkansas, *E. J. Palmer*, April 27, 1914 (no 5396), October 19, 1914 (no. 6878), April 10 and 12, 1915 (nos. 7172, 7184), June 17, 1915 (no. 8032), October 18, 1915 (no. 8952).

This tree, which in the size and thickness of the involucre produces remarkable fruit, long puzzled Mr. PALMER and me until the unfolding leaves showed its relationship with *Carya Buckleyi*.

A hickory tree which is common and widely distributed in Missouri and northwestern Arkansas has the peculiar rusty brown pubescence of the Texas hickory on its young leaves and branchlets and on its winter-buds, and although the fruit is smaller this tree cannot be specifically distinguished from that species, and is here treated as

CARYA BUCKLEYI var. **villosa,** nov. comb.—*Hicoria glabra* var. *villosa* Sargent, Silva N. Am. **7**:167. *pl. 355.* 1895; *Hicoria villosa* Ashe, Bull. Torr. Bot. Club **24**:481. 1897; Sargent, Man. 145 (in part). 1903; *Carya villosa* Schneider, Ill. Handb. Laubholz. **1**:803. 1906; *Carya glabra* var. *villosa* Robinson, Rhodora **10**:32. 1908.—Differing from the type in its smaller obovoid or ellipsoidal fruit with a thinner often indehiscent involucre.

A single tree, the type of this variety, was found nearly 40 years ago by the late GEORGE W. LETTERMAN on a dry rocky hillside at Allenton, St. Louis County, Missouri, where it is still growing. LETTERMAN considered it a hybrid. Before the Texas hickory and its varieties were recognized it was considered a variety of *Carya glabra*, from which it differs in its pubescence and in its usually more dehiscent involucre. There would be more reason in following ASHE and treating it as a species did not trees occur with fruit which approaches in its larger size and thicker involucre that of the var. *arkansana* which occasionally grows with it in Missouri.

The Allenton tree has thick, rough, deeply furrowed, nearly black bark similar to that of *C. Buckleyi* as it grows near Denison, Texas. On trees growing in better soil in other parts of the state the bark is often paler and less deeply furrowed. The leaves of the typical tree are 5–7-foliolate, with pubescent petioles and rachis, becoming glabrous or nearly glabrous; the leaflets are lanceolate to oblanceolate, long-pointed, with prominent reticulate veinlets, the lateral nearly sessile, the terminal short-petiolulate, nearly glabrous above and early in the season covered below with rusty pubescence and small brownish scales, in the autumn glabrous or nearly glabrous with the exception of the fascicled hairs on the lower side of the midrib. The fruit of the Allenton tree is obovoid, cylindrical, sometimes slightly winged above the middle, about 2.5 cm. long and 1.8 cm. in diameter, rusty pubescent and covered with scattered yellow scales; the involucre is about 2 mm. in thickness and is indehiscent or splits tardily to the base usually only by 2 sutures. The nut is ovoid, rounded at base, pointed at apex, only slightly angled, thin-shelled, and faintly tinged with red. The branchlets are slender, pubescent during their first year and puberulous in their second season. The winter-buds are covered with rusty brown pubescence and yellow scales, and often furnished near the apex with the tufts of white hairs, which are generally found on the buds of *Carya Buckleyi*. The fruits on trees in other parts of the state vary from obovoid to ellipsoidal, or are rarely subglobose; they vary from 1.5 to 3 cm. in length, and are nearly cylindrical or much compressed; the involucre varies from 1 to 4 mm. in thickness, and on some trees the fruit is completely covered by the yellow scales. On some trees the branchlets lose their pubescence early and by the end of September are glabrous, red, and lustrous.

I have seen specimens of this tree collected in Missouri by the Reverend *John Davis* in the neighborhood of Hannibal, Marion County (nos. 1361, 1630, 2028, 2032, 2078, 2089, 2156, 2160, 2162, 2163, 2166, 2182, 2188, 2190, 2237); in Grain Valley, Jackson County, *B. F. Bush*, May 24, 1913 (nos. 6981, 6991); at Jerome, Phelps County, *J. H. Kellogg*, May 7, 1913 (nos. 333, 339, 340, 341, 347, 348, 357); Allenton, St. Louis County, *G. W. Letterman*, June 20, 1880, May 15, 1881, May 1, 1882, April 1883, July 16, 1911, May 10, 1912, *J. H. Kellogg*, October 7, 1911, *E. J. Palmer*, August 13, 1917 (no. 12652); Des Arc, Iron County, *E. J. Palmer*, July 2, 1914 (no. 6165); Branson, Tenney County, *E. J. Palmer*, October 23, 1913 (no. 4707), June 18, 1914 (no. 5891); Willow Springs, Howell County, *E. J. Palmer*, July 8, 1914 (no. 6227); dry hillsides near Campbell, Osage County, *C. S. Sargent*, September 5, 1915; dry barren hills, Joplin, Jasper County, *E. J. Palmer*, October 1911 (no. 3494), May 17 and September 18, 1913 (nos. 3491, 3928, 4356, 4357, 4358, the last with ellipsoidal fruit on a long peduncle, 4359, 6890, 6891); Noel, McDonald County, *E. J. Palmer*, September 6 and 14, 1913 (nos. 4060, 4159, 4170, 4216, 4336, 4337, 5410).

ARKANSAS: Eureka Springs, Carroll County, *E. J. Palmer*, September 22 and 24, 1913 (nos. 4428, 4482), May 11, 1914 (no. 5548).

HYBRID HICKORIES.—The supposed hybrids between species of *Apocarya* are

CARYA BROWNII Sargent, Trees and Shrubs **2**:195. *pl. 178.* 1913. —This tree grows on the bottom lands of the Arkansas River below Van Buren, Crawford County, Arkansas. In the Arboretum Collection are nuts of what is no doubt the same hybrid collected at Collinsville, Rogers County, Oklahoma. To this hybrid probably belongs the so-called Galloway hickory (see S. GALLOWAY in Gardening **2**:26. 1874; TRELEASE in Rep. Mo. Bot. Gard. **7**:33. *pl. 16. figs. 15, 16. pl. 20;* Sargent, *l.c.* 196).

A tree evidently of the same parentage has been described as

CARYA BROWNII var. VARIANS Sargent, Trees and Shrubs **2**:196. 1913.—This tree grows on the banks of Sears Creek near the Pump House of the Van Buren Water Works, Crawford County, Arkansas. A tree with similar fruit has been found near Natchez, Adams County, Mississippi, by Miss C. C. COMPTON.

Three evident hybrids between species of *Apocarya* and *Eucarya* are known.

CARYA LANEYI Sargent, Trees and Shrubs **2**:196. 1913.—This appears to be a hybrid of *C. cordiformis* and *C. ovata*. The original tree is in the Riverside Cemetery at Rochester, New York. In the Arboretum Collection there are nuts of a tree growing at Millersville, Lancaster County, Pennsylvania, which is known as the Beaver hybrid and appears to be of the same parentage. Trees of the same parentage but with the leaves of *C. cordiformis* and with larger fruits with thicker involucres than those of that species and nuts resembling those of *C. ovata* have been distinguished as

CARYA LANEYI var. CHATEAUGAYENSIS Sargent, *l.c.* 1913.—First discovered at Chateaugay near the mouth of the Chateaugay River in the Province of Quebec by Professor J. G. JACK, this tree was later found by him at Summertown, Ontario.

Carya Schneckii, n. hyb. (*C. alba×pecan*).—Leaves 7–9-foliolate, glabrous; leaflets thin, acuminate at apex, cuneate and unsymmetrical at base, falcate, short-petiolulate. Fruit oblong, acute at apex, rounded at base, pubescent, 5.5 cm. long, with an involucre splitting to the base and 6–7 mm. in thickness; nut oblong, gradually narrowed and rounded at base, acuminate at apex, slightly compressed, angled to the middle or to the base, reddish and conspicuously streaked with brown, 4–4.5 cm. long and about 2 cm. wide, with a shell 1–2 mm. in thickness and a sweet kernel.

A large tree with bark resembling that of the pecan, stout reddish brown puberulous branchlets, and winter-buds with imbricated scales, the outer dark red-brown and puberulous, the inner thickly covered with hoary tomentum; axillary buds solitary with usually valvate scales.

Lawrenceville, Lawrence County, Illinois, *Dr. J. Schneck*, October 15, 1895 (type) (see Sargent, Silva N. Am. **7**:138). A tree believed to have been of the same parentage was found at about the same time by Mr. F. REPPERT near Muscatine, Muscatine County, Iowa (see TRELEASE in Rep. Mo. Bot. Gard. **7**:39. *pl. 23. figs. 2–5*).

Carya Nussbaumerii, n. hyb. (*Carya laciniosa*×*pecan*).—Leaves 7–9-foliolate; petioles and rachis puberulous; leaflets lanceolate, long-pointed and acuminate at apex, rounded and unsymmetrical at base, pubescent on the lower surface, the terminal petiolulate, the lateral nearly sessile. Fruit oblong, narrowed and rounded at base, acute at apex, puberulous and more or less thickly covered with yellow scales, about 7 mm. long and 3.5–3.8 cm. in diameter; involucre splitting nearly to the base and 4 mm. in thickness. Nut oblong, compressed, only slightly angled, short-pointed at apex, rounded at base, 6 mm. long, 3.5 cm. wide, and 2.5 cm. thick, with a shell 1.5–2 mm. in thickness.

I suggest this name for the Nussbaumer hybrid (see SARGENT, Silva N. Am. **7**:158. *pl. 349. fig. 4;* TRELEASE in Rep. Mo. Bot. Gard. **7**:41. *pls. 22, 23. figs. 7–9*).

This tree was first found on the bottoms between Mascoutah and Fayetteville, St. Clair County, Illinois. A tree producing a similar nut which came originally from Illinois was cultivated before 1892 by Mr. R. M. FLOYD of Cedar Rapids, Iowa, and has been called the Floyd nut. In October 1895 Dr. SCHNECK found a tree producing similar fruit at Mt. Vernon, Posey County, Indiana. Grafted plants of this tree, which has been called the McCallister (see Nut culture in the United States, Bull. U.S. Dept. Agric., Div. of Pomology, 1896, 63. *pl. 9. fig. 6*), were sent to Washington, Georgia, whence this tree was distributed as the Washington nut, a name now abandoned by pomologists. Another of these trees has been reported from the neighborhood of Burlington, Des Moines County, Iowa, and another, known as the Rockville nut, from near Rockville, Bates County, Missouri. In its foliage and in the color of the branchlets this hybrid resembles *C. laciniosa*. The branchlets, however, are not as stout and are less pubescent than those of that species, and the buds are smaller and more acuminate. The fruit in shape resembles that of the pecan, but does not have the sutural wings of that species, and the nut is white or nearly white and only slightly streaked with brown.

Carya Dunbarii, n. hyb. (*C. laciniosa*×*ovata*).—I suggest this name for a number of trees found growing on the bottoms of the Genesee River at Golah, Monroe County, and Mount Morris, Livingston County, New York, by John Dunbar, assistant superintendent of the parks of the city of Rochester, New York. These trees, which have at different times been considered both *C. laciniosa* and *C. ovata*, vary among themselves in the color and pubescence of the branchlets, in the size of the buds, and in the size and shape of the fruit and nuts. The leaves have the 7 or 9 leaflets of *C. laciniosa*, but the leaflets are usually narrower than those of that species and less pubescent. I have selected no. 68 *Dunbar*, September 19, 1911, as the type of this hybrid, as the tree is still standing and can easily be located.

Leaves 7-foliate, the petioles and rachis slender, glabrous; leaflets acuminate, puberulous on the lower surface and pubescent on the under side of the midribs, the terminal oblong-obovate, cuneate, and gradually narrowed below into a slender petiolule 1.5 cm. in length, the lateral lanceolate to oblanceolate, nearly sessile. Fruit oblong, rounded at ends, glabrous, 4 cm. long, 3 cm. in diameter; involucre splitting to the base, 5 mm. in thickness; nut oblong, gradually narrowed and rounded at base, acute at apex, compressed, conspicuously ridged to below the middle, pale brown, 3 cm. long, 2.5 cm. wide, and 2 cm. thick.

A tree 80–90 ft. high, with light gray scaly bark, stout spreading branchlets puberulous early in the season, glabrous and pale red-brown in the autumn. Terminal buds, oblong, acute, 1.5–1.8 cm. long and 6–7 mm. in diameter, the outer scales dark red-brown and puberulous.

Golah, Monroe County, New York, *J. Dunbar*, September 19, 1911 (no. 68, type).

No. 71 Golah, collected by *J. Dunbar* September 19, 1911, has the leaves in the size and shape of the leaflets like those of *C. ovata;* the petioles and rachis are pubescent, and the leaflets are more pubescent than those of no. 68. The fruit is oblong-obovoid, compressed, rounded at base, abruptly acute at apex, 4 cm. long, 3 cm. wide, and 2 cm. thick, with an involucre splitting nearly to the base and 4 cm. thick. The nut is oblong-obovoid, acute at the ends, only slightly angled, and pale in color.

This tree, which is still standing, is 80 ft. high, with ashy gray bark divided into plates but not separating into loosely attached scales like that of its supposed parents, and stout reddish glabrous branchlets. The terminal winter-buds are acute, 1.8 cm. long, the outer scales pale pubescent, the inner hoary tomentose. In the number of leaflets the leaves of this tree resemble those of *C. laciniosa*, but in the shape of the leaflets they resemble those of *C. ovata* var. *fraxinifolia*. In shape the fruit resembles a small fruit of *C. laciniosa*, but the involucre is thinner than that of *C. ovata* or *C. laciniosa*. The nut is more like that of *C. laciniosa;* the bark and color of the branchlets are unlike those of either of the supposed parents. The winter-buds are more like those of *C. laciniosa* than of *C. ovata*.

No. 61 Golah, *J. Dunbar*, September 29, 1911, has the leaves of *C. laciniosa*, short-oblong fruit 4 cm. long, depressed at the apex like that of *C. ovata*, with an involucre 6 mm. in thickness. The branchlets are red and glabrous and unlike those of either parent. Except in the branchlets this number resembles a small-fruited *C. laciniosa*.

No. 66 Golah, *J. Dunbar*, September 19, 1911, has the leaves of *C. laciniosa*, oblong slightly obovoid pubescent fruit only 3 cm. long, with an involucre 4 cm. in thickness, and a compressed slightly angled reddish nut. The branchlets are reddish, pubescent, and about as thick as those of the common form of *C. ovata*. The buds are acute and 7–8 mm. long, with puberulous outer scales.

No. 73 Golah, *J. Dunbar*, September 19, 1911, has the leaves of *C. laciniosa*, fruit similar to that of no. 66 and slender, densely pubescent brown branchlets resembling those of a pubescent form of *C. ovata*.

No. 207 Golah, *J. Dunbar*, September 19, 1911, has the leaves of no. 68, fruit like no. 61, stout glabrous red branchlets and terminal buds 1.5 cm. long, the outer scales covered with pale pubescence.

No. 208 Golah, *J. Dunbar*, September 19, 1911, has leaves resembling in shape those of *C. ovata*, fruit like that of no. 73 and 3 cm. long; branchlets somewhat stouter and less pubescent than those of no. 73, and the winter-buds of *C. ovata*.

No. 250 Golah, *J. Dunbar*, August 31, 1915, has the leaves of *C. laciniosa*, obovoid pubescent fruit 3–3.5 cm. long, with an involucre 5 mm. in thickness, and a slightly compressed angled nut. The branchlets resemble those of the pubescent form of *C. ovata*.

No. 251 Golah, *J. Dunbar*, August 31, 1915, has only slightly pubescent leaves with leaflets resembling in shape those of *C. ovata* var. *fraxinifolia*. The fruit is pubescent, subglobose, 3 cm. long and rather broader than long, with an involucre 3 mm. in thickness; the nut, although less prominently ridged, resembles the nut of *C. ovata*. The branchlets are reddish brown and puberulous.

No. 252 Golah, *J. Dunbar*, August 31, 1915, has the leaves of *C. laciniosa*, oblong pubescent fruit 3 cm. long, with an involucre 5 mm. in thickness and conspicuously angled nuts. The branchlets are stout, dark red-brown, and densely pubescent. The terminal bud is about 1 cm. in length. Except in the color of the branchlets, the small size of the buds, and in the small size of the fruit, this number resembles *C. laciniosa*.

No. 253, *J. Dunbar*, August 31, 1915. Although only puberulous, the leaves otherwise generally resemble those of *C. laciniosa*. The fruit is similar to that of no. 73, but the involucre is 7 mm. in thickness; the nut is only slightly compressed and angled. The branchlets are reddish brown, pubescent, and as stout as those of the common form of *C. ovata*. The bud is 1 cm. long with pubescent outer scales.

No. 254 Golah, *J. Dunbar*, August 31, 1915, has leaves resembling those of no. 68, the fruit of *C. laciniosa*, and red nearly glabrous winter branchlets. The winter-buds are 1 cm. long with puberulous outer scales.

No. 59. Mount Morris, Livingston County, *J. Dunbar*. This has leaves like no. 68 from Golah; the fruit is that of *C. laciniosa* and 4 cm. long. The branchlets are slender, reddish, and glabrous; the winter-buds are about 1 cm. in length with pubescent outer scales.

There is so much variation in these trees that their hybrid origin seems probable. The most remarkable things about them are the red glabrous lustrous branchlets of some of the trees; these are entirely unlike those of either of the supposed parents and suggest that one of the forms of *C. ovalis* or *C. glabra* might have had some influence on them. If they are hybrids in large part between

C. laciniosa and *C. ovata*, as I believe, they are the only hybrids between two species of *Eucarya* which have been noticed, other hybrids of *Carya* having been produced by the crossing of 2 species of *Apocarya* or of a species of *Apocarya* with a species of *Eucarya*. In the case of other hybrids of *Carya* only a single tree or single trees in different locations have been noticed. The hickory trees in western New York, however, have been more carefully examined by Mr. DUNBAR and his associates than the hickories in any other part of the United States. When the trees in other parts of the country are as carefully and intelligently studied, it is possible that many hybrid hickories and many individuals of these hybrids will be found, just as in recent years many hybrid oaks often with numerous individuals have been found.

ARNOLD ARBORETUM
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FERTILIZATION IN LILIUM

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 243

WANDA WENIGER

(WITH PLATES XI–XIII)

Introduction

The cytological phenomena of fertilization have been studied with greater detail in the gymnosperms than in the angiosperms. This paper is the result of an attempt to discover whether there is a similarity between the process of fertilization as already described for gymnosperms and that of angiosperms. *Lilium* has long been the type used in the study of fertilization in the classroom; it was chosen for the subject of study in this case because it lends itself particularly well to cytological work. The writer is indebted to Dr. C. J. CHAMBERLAIN for the suggestion of the problem and for his helpful assistance throughout the progress of the work.

In *Pinus* (**1, 3, 5, 7, 8**), *Tsuga* (**14**), *Juniperus* (**18, 19**), and *Abies* (**12**) evidence has been brought to bear upon the fact that no fusion of the male and female chromatic substance takes place.

BLACKMAN (**1**), in 1898, described the cytological features of fertilization in *Pinus silvestris*. While the outlines of the 2 sexual nuclei are still visible, the chromosomes are found in 2 separate clumps; and even on the spindle fibers of the first division they can be distinguished into 2 groups. After a longitudinal splitting the half chromosomes fuse together in the telophase of the division.

CHAMBERLAIN'S (**3**) account of oogenesis in *Pinus Laricio* includes figures of the male and egg nuclei. He states that after the male pronucleus is within the oosphere nucleus the chromatin of the 2 pronuclei appears as 2 distinct masses in the spireme stage. "Perhaps segmentation of the 2 spiremes occurs while they are still separate." In *Tsuga canadensis* MURRILL (**14**) reports 2 sets of chromosomes distinct in the equatorial region of the first spindle.

Miss FERGUSON (7), in her first paper on *Pinus Strobus* in 1901, finds that the 2 chromatic groups are distinctly recognizable at the time of the segmentation of the spiremes, and can still be clearly made out during the early development of the chromosomes, but not as late as the equatorial plate stage. "There is never any fusion, as ordinarily understood, of the male and female nuclei." In her second paper on *Pinus* Miss FERGUSON (8) describes the longitudinal splitting of the 24 chromosomes on the equatorial plate. According to NORÉN (18, 19), the essential features of fertilization in *Juniperus communis* are similar to those of *Pinus*.

A very detailed account of fertilization is given by HUTCHINSON (12) for *Abies balsamea*. Two groups of chromatin at the micropylar end of the egg nucleus, one male and the other female, become separated into 16 chromosomes each, and these pass on to the spindle fibers. The 2 spindles in the metaphase fuse, and the chromosomes are arranged to form 16 pairs, each pair forming a C, in which the 2 chromosomes are twisted about each other. By means of a transverse break at the angle of the bent chromosomes each pair forms 4 segments. Of the 64 segments, 32 go to each pole, where in the daughter nuclei they remain very distinct.

CHAMBERLAIN counted 12 chromosomes in *Stangeria* (4) at the equatorial plate stage of the division of the fertilized egg, while the sporophyte number is 24. He accounts for the haploid number by assuming the chromosomes to be of a double character, and supports HUTCHINSON's view of the pairing of chromosomes.

In angiosperms the behavior of the chromatin during fertilization has received little attention. In the majority of cases the statement is made that the nuclei fuse while in the resting condition almost immediately after they come in contact and form a definite resting nucleus, differing only in its greater size from the unfertilized egg nucleus.

GUIGNARD's (9) paper in 1891 on fertilization in *Lilium Martagon* contains statements overlooked by most writers. The formation of 2 distinct spiremes in the male and egg nuclei was observed but not figured. No fusion is brought about between the chromatin of the 2 nuclei, even when the nuclear membranes disappear. The segments of each spireme pass on to the equatorial plate, where each splits longitudinally. In 1895 MOTTIER (**13**) first described the vermiform shape of the male nuclei in *Lilium Martagon*. The male and egg nuclei fuse in the resting condition after coming in contact and are figured as forming a resting nucleus. In 1898 NAWASCHIN (**15**) announced the discovery of double fertilization in *Lilium Martagon* and *Fritillaria tenella*. The male nucleus that fuses with the polar nuclei loses its spiral form, but the 3 nuclei remain distinct until the prophase of the division. The fusion of the 3 nuclei occurs when the numerous chromosomes come together on the equatorial plate. "Fusion occurs, not in the resting stage, as MOTTIER indicates, but in the prophases of the division, as GUIGNARD first observed."

The motility of the male nuclei is described for *Lilium Martagon* and *Fritillaria tenella* by NAWASCHIN (**16, 17**); for the tulip by GUIGNARD (**11**); and for *Lilium Martagon* and *L. auratum* by BLACKMAN and WELSFORD (**2**), and Miss WELSFORD (**23**). These authors attribute independent motion to the male nuclei.

In *Paris quadrifolia* and *Trillium grandiflorum* ERNST (**6**) finds a striking difference between the fusion of the male nucleus with the egg and that with the polar nuclei. In the former case the fusion is complete, so that a typical resting nucleus is formed. In the latter case the polar nuclei begin to form spiremes even before the male nucleus arrivės, and in the group of the 3 nuclei (the 2 polar nuclei and the male nucleus) 3 spiremes are distinguishable.

Distinct maternal and paternal chromosomes were first described for an angiosperm by Miss PACE (**21**). She found spiremes in all nuclei of the embryo sac of *Cypripedium* before fusion took place. The spireme was well formed in every nucleus, and shortened almost enough to segment into chromosomes. "It would seem in this case, that if fusion does take place, there could be no possibility of a fusion of the chromatin, which would certainly divide into chromosomes from the spireme as it is now formed."

NAWASCHIN (**17**) published another paper on *Lilium Martagon* in 1910, again emphasizing the fact that the mature nuclei are capable of movement. He finds that the mitosis of the 2 male nuclei in the pollen tube is characterized at an early stage by sharply differentiated chromosomes, so that the sperm nuclei do not reach the resting stage, but remain in the condition characteristic of a telophase.

Recently SAX (**22**) has investigated *Fritillaria pudica*. In most cases it is not until the male nucleus and the egg nucleus have completely fused that he finds any appearance of the formation of the spireme. In rare cases, however, the spireme stage is found while the 2 nuclei are still distinct in outline. He believes that the rare appearance of such cases is probably of little significance, since it is probable that these nuclei subsequently fuse completely because no later stages were found in which fusion was incomplete. From the many stages and abundant cases of triple fusion he observed he thinks there is no doubt that the 2 polar nuclei and the male nucleus fuse completely and that the subsequent division is normal.

Methods

Stages in fertilization were obtained from ovaries of *Lilium philadelphicum* collected in the field near Osborn, Calumet, and Pine, Indiana, in June and early July, 1916, at the time when the petals "snapped," and after the petals had fallen. To correlate the time of pollination with stages in fertilization, flowers were brought into the laboratory, pollinated, and kept under bell jars for several days, until fertilization had taken place. In general, it may be said that the petals drop on the third day after pollination, and the style separates from the ovary on the fourth or fifth day. The male nucleus was in contact with the egg nucleus from 60 to 72 hours after pollination.

The material for *Lilium longiflorum* was obtained from plants grown in the greenhouse. It produced seeds readily, although it is generally reported not to set seed. The male nucleus was in contact with the egg nucleus about 120 hours after pollination. Of the upward of 500 cases of fertilization observed in these 2 species, the majority showed the male and egg nuclei in contact, with their chromatin in early prophases of the division.

Chrom-acetic-osmic and Flemming's medium solutions were used as fixatives, and the ovaries trimmed so as to permit more rapid penetration of the embryo sacs. Sections were cut 10 μ thick and stained with Flemming's triple stain or Haidenhain's iron-alum-haematoxylin.

Observations

Upon leaving the pollen tube the male nuclei retain their coiled shape for some time. The egg nucleus (fig. 1), with chromatin in a resting condition before the arrival of the male nucleus, remains in this condition, while the male nucleus lies in contact with it. Stages can be found abundantly in which the male nucleus has penetrated the egg and lies adjacent to the egg nucleus, and in which the chromatin of the former is in an early prophase (fig. 2), or spireme stage (fig. 3), while the chromatin of the latter more lightly staining nucleus is in the resting stage. The male nucleus is more or less curved around one side of the egg nucleus and usually measures about 9 μ at its short diameter, while the spherical egg nucleus is 10–12 μ in diameter. Soon the male nucleus becomes more rounded, as is shown in fig 4, where the chromatin in both nuclei is still in the same stage as in fig. 3.

The chromatin of the egg nucleus is then formed into a spireme (figs. 5, 6); but this spireme was never found to stain as densely or become as regular as that of the male nucleus. The membranes of the 2 nuclei seem still to be in contact at this stage. No fusion of the spiremes takes place, but each is segmented into chromosomes independently. This account agrees with that of GUIGNARD for *Lilium Martagon*, where no fusion takes place between the chromatic elements of the 2 nuclei.

In the gymnosperms investigated the separate groups of chromosomes formed from the male and female spiremes respectively become oriented on separate spindles, and then the 2 spindles fuse during the metaphase. Whether or not this is true for *Lilium* has not been determined. The entire process of fertilization in *Lilium* is an exceedingly rapid one, since the time elapsing between the discharge of the male nuclei and the formation of the 2-celled embryo is probably not longer than 8 hours. Since the contact stage of the 2 nuclei in the prophases of the division is of such relatively common occurrence in preparations made, it would seem that it occupies the greater part of this time, and that for this reason the actual division of the fertilized egg is a very difficult stage to obtain. One very favorable preparation shows this division, with some of the chromosomes still on the equatorial plate and others already near the poles of the spindle. Figs. 11, 12, and 13 represent the 3 sections of this spindle, and in fig. 14 the 3 drawings are superimposed and slightly diagrammed. Of the 24 chromosomes present on the equatorial plate, 12 are contributed by the male nucleus and 12 by the egg nucleus. The chromosomes are not drawn into the sharp U's and C's so characteristic of divisions in *Lilium*. The chromosomes come together in pairs in which they twist more or less about each other (fig. 12*a*). Each of the chromosomes of the 12 pairs then breaks transversely at the center of the ellipse it forms, each pair giving rise to 4 segments. The 48 segments in the form of small rods remain paired (fig. 12*b*, *c*) as they move toward the poles of the spindle. The components of each pair are similar in size so far as could be determined; one segment is male and the other female in origin. In fig. 14 the 12 pairs of chromosomes are represented, with the 4 segments of a pair indicated by the same number. All segments going to one pole are in black, those to the opposite pole in outline. Chromosomes 8 and 12 have not as yet come in contact and the transverse break has not yet appeared. This behavior of chromosomes resembles that of the first reduction division in tetrad formation. There is a pairing of chromosomes and a subsequent transverse breaking. The result of the division is not the reduced number of chromosomes, however, but the diploid number, for only a transverse break occurs, and no further splitting.

In the telophase of this division (figs. 15, 16) no further evidence of the pairing of the chromosomes could be observed. It would seem probable that the individuality of the chromosomes derived from the male and egg nuclei would persist. The second division (fig. 17) of the fertilized egg is in all respects like the ordinary vegetative division in *Lilium*, with a longitudinal splitting of the characteristic U-shaped chromosomes during the metaphase.

Observations were also made on the behavior of the chromatin during triple fusion. The process occurs much more rapidly and the resulting nucleus divides at least twice before the fertilized egg undergoes division. At the time that the endosperm nucleus divides (fig. 7) the male and egg nuclei are still in the stage shown in fig. 3 or 4. The 2 polar nuclei, with membranes distinct, are in the resting condition when the male nucleus in the spireme stage comes in contact with them (fig. 8). A spireme is then formed in each polar nucleus also (fig. 9), and the nuclear membranes disappear at the point of contact of the nuclei. The lower polar nucleus is usually a little larger than the one coming from the micropylar end of the embryo sac. The male nucleus is at the left in fig. 9.

Segmentation of spiremes occurs so that on the spindle (fig. 19) the chromosomes are extremely long and U-shaped. The number of segments is difficult to ascertain, but it approaches the $3x$ number. The division is accomplished by a longitudinal splitting of chromosomes, producing in the anaphase a mass of long bent segments that cannot be counted with any satisfaction.

There is a striking difference between the first division of the fertilized egg and that of the endosperm nucleus. The former is characterized by shorter straighter chromosomes, a pairing of chromosomes, and a subsequent transverse breaking of each pair to form 4 segments, of which 2 go to each pole. The division of the endosperm nucleus resembles the ordinary vegetative division by means of a longitudinal splitting of chromosomes. The number of chromosomes is $3x$. Since previous cytological work has not covered the necessary phases, it is possible that the description of the behavior of chromosomes during the first division of the fertilized egg here given may apply quite generally to angiosperms. A longitudinal splitting of chromosomes on the equatorial plate would bring about the same result in that the $2x$ number of chromosomes goes to each of the daughter nuclei; but the supposition of a longitudinal splitting would not account for the situation described. If a longitudinal splitting should occur before the transverse breaking, rather than a pairing of chromosomes, the resulting number would be 96 rather than 48 segments.

The 3 phases of fertilization, union of cells, union of nuclei, and union of chromosomes, occur in rapid succession in animals, since the reduction division immediately precedes fertilization. In plants the 3 processes may be separated for a longer or shorter period. In the rusts there is a long gap between the union of the gametes at the base of the aecidium and the nuclear and chromosome conjugation. In some of the green algae, such as *Oedogonium*, the 3 come close together, since reduction follows soon after fertilization. In the brown algae the 3 are also close together, but reduction precedes fertilization. In the higher plants cell and nuclear union have been thought to come close together at the beginning of the sporophyte generation, while the chromosome union did not occur until during the reduction division at the end of the sporophyte generation. In *Abies*, as found by HUTCHINSON; in *Stangeria*, according to CHAMBERLAIN; and in *Lilium* there seems to be evidence of a chromosome union at the time of fertilization.

Summary

1. The egg nucleus is in a resting condition when the male nucleus, in spireme stage, comes in contact with it.

2. Distinct male and female spiremes are formed which are segmented into chromosomes while the nuclei are in contact.

3. On the equatorial plate the male and female chromosomes come together in x number of pairs and divide by means of a transverse break, each pair forming 4 segments. The segments move to the poles in pairs. Of the $4x$ segments formed, $2x$ go to each pole of the spindle.

4. The chromosomes on the equatorial plate of the second division of the fertilized egg divide longitudinally.

5. The endosperm nucleus divides at least twice before the fertilized egg undergoes division.

6. A distinct spireme is formed in each of the nuclei of the triple fusion, and the $3x$ segments are oriented on the equatorial plate.

7. The endosperm nucleus divides in the typical vegetative manner by means of a longitudinal splitting of the chromosomes.

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EXPLANATION OF PLATES XI-XIII

All drawings were made with an Abbé camera lucida at table level and Zeiss apochromatic objectives and compensating oculars. For fig. 7 the 8 ocular and 2.0 mm. objective were used, giving a magnification of 1500; for the remainder of the drawings the 18 ocular was used with the 2.0 mm. objective, and the magnification was 4000. All drawings were reduced one-half in reproduction.

PLATE XI

FIG. 1.—Egg before fertilization, with nucleus in resting condition; ×2000; *L. philadelphicum.*

FIG. 2.—Male nucleus in early prophase; egg nucleus in resting condition; ×2000; *L. philadelphicum.*

FIG. 3.—Chromatin of egg nucleus more irregular; male nucleus still curved around egg nucleus; ×2000; *L. philadelphicum.*

FIG. 4.—Male nucleus rounded; ×2000; *L. longiflorum.*

FIG. 5.—Early spireme in egg nucleus; ×2000; *L. philadelphicum.*

FIG. 6.—Distinct spiremes in male and egg nucleus; segmentation begun; ×2000; *L. longiflorum.*

FIG. 7.—Endosperm nucleus undergoing division while egg nucleus is in resting stage and male nucleus in contact with it shows a spireme; ×750; *L. philadelphicum.*

PLATE XII

FIG. 8.—Triple fusion: male nucleus in spireme stage, upper and lower polar nuclei with chromatin in resting stage; ×2000; *L. longiflorum.*

FIG. 9.—Distinct spiremes in 3 nuclei of triple fusion; male nucleus at upper left; ×2000; *L. philadelphicum.*

FIG. 10.—Metaphase of endosperm nucleus; ×2000; *L. philadelphicum.*

FIG. 17.—Second division of fertilized egg; ×2000; *L. longiflorum.*

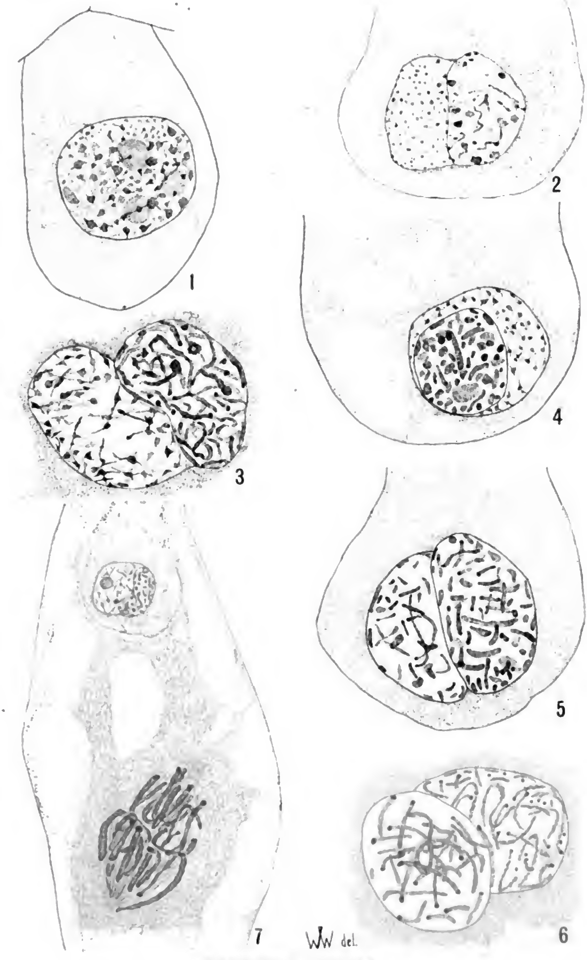
PLATE XIII

FIGS. 11-13.—Three sections of spindle of fertilized egg in division, showing pairing of chromosomes, transverse break, moving of pairs to the poles; ×2000; *L. longiflorum.*

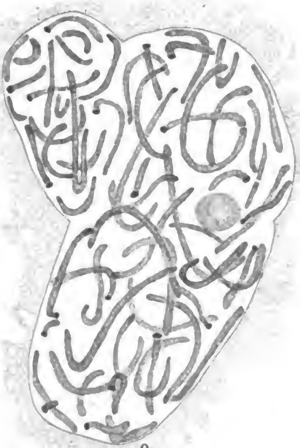
FIG. 14.—Diagram of division of fertilized egg, made by superimposing figs. 11-13; the 12 pairs of chromosomes are represented, with 4 segments of a pair indicated by the same number; segments in solid black go to one pole, while those in outline go to the other pole; chromosomes numbered 8 and 12 have not yet paired or segmented.

FIG. 15.—Early telophase of first division; ×2000; *L. longiflorum.*

FIG. 16.—Late telophase of first division; ×2000; *L. longiflorum.*



WENIGER on LILIUM



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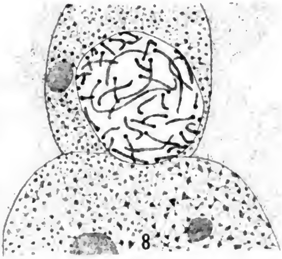

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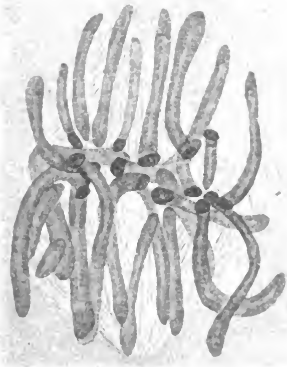

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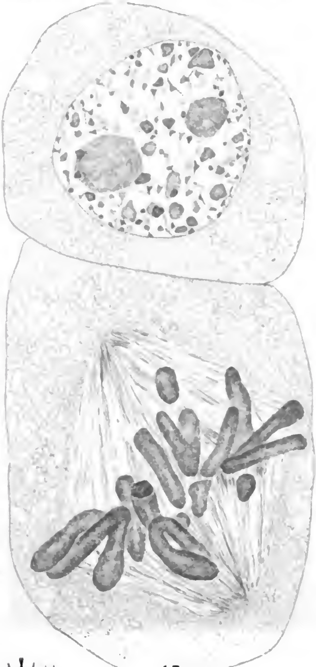

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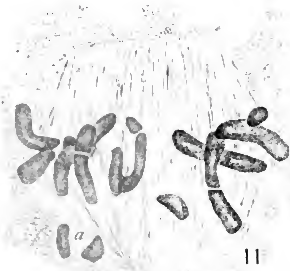
WW del.

WENIGER on LILIUM



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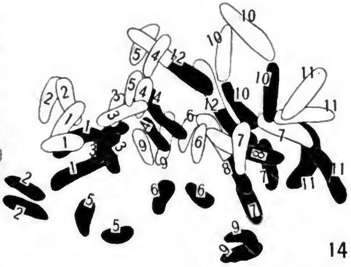

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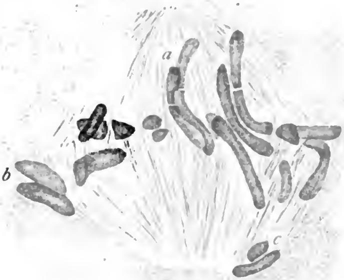

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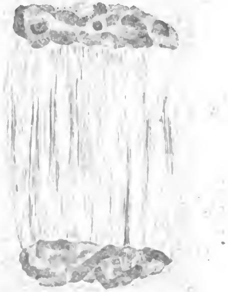

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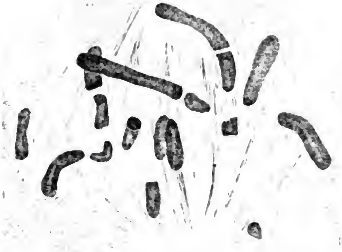
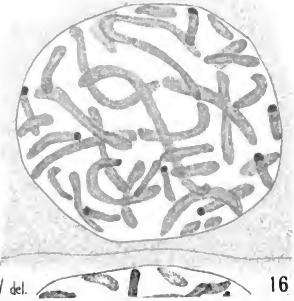


13 WW del.



16

WENIGER on LILIUM

ABNORMAL CONJUGATION IN SPIROGYRA

J. G. Brown

(WITH THREE FIGURES)

Recently while teaching a class in plant histology, the attention of the writer was directed by one of his students to the conjugating cells of *Spirogyra* shown in the accompanying figures. The material from which the figures were drawn, which answered to Wolle's description of *S. nitida*,[1] was collected in the Rillito River north of Tucson in April 1917. When they were examined under low power lens, the conjugating cells shown in fig. 1 presented the appearance of a knot. Upon analyzing the situation, one of the four cells was found to have connections with three others, two with

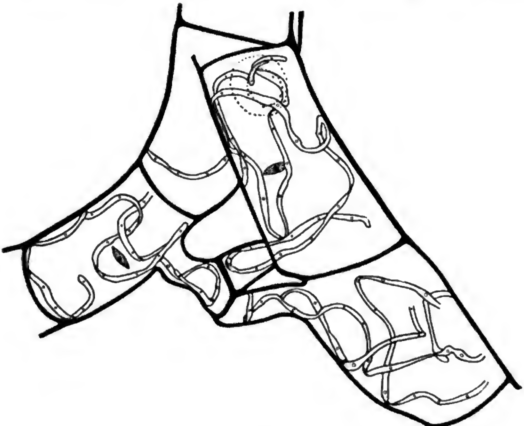


Fig. 1

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[1] Wolle, Francis, Fresh-water algae of the United States, p. 217.

two others, and the fourth with one other. Three of the conjugation branches formed a triple connection, and two other cases of triple connection were found on the same slide. The cells represented in fig. 2 also presented an interesting study in reproduction. One cell was here monopolizing the energies of two cells in an adjacent filament, while its neighbor on each side had resorted to parthenogenesis. Although several slides were examined, no cases of lateral conjugation were observed.

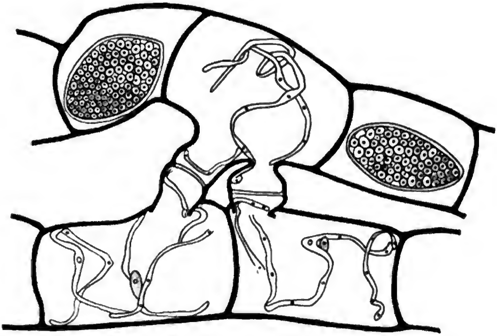

FIG. 2

Abnormal conjugation in other species of *Spirogyra* has been mentioned by several investigators, notably by the WESTS,[2] who have examined material from many different countries. Several types of scalariform conjugation between three cells have been described: (*a*) by means of four branches connecting three cells belonging to two different filaments; (*b*) by means of four branches connecting three cells belonging to as many different filaments; (*c*) by means of three branches forming a triple connection. According to the WESTS the last type mentioned is very rare. They illustrate a case of triple connection of conjugation branches in *S. condensata* in which one of the three branches has prevented the protoplasts of two of the three cells concerned from fusing. This appears to be a common result, and the large proportion of failures has been interpreted as proving the abnormality of the method. Another illustration included in the paper cited represents a condition in *S. maxima* similar to the one described in this note in fig. 2 for *S. nitida*, excepting the parthenogenetically formed spores. The great profusion of conjugation branches exhibited occasionally by *Spirogyra* filaments, accompanied by the tendency to form abnormal connections, has been regarded as a response to environmental conditions exceptionally unfavorable for vegetative growth. In this region such external factors as the volume, temperature, and salt content of water are extremely variable. The fluctuation in water volume may be such that in a few days a large, rapidly flowing stream is changed to a trickling brook, then to a series of stagnant pools, then later to a "dry river" carrying its entire flow beneath the surface of the bed. In the winter snow water reaches the foothill and mesa country in a cold condition after showers in the mountains. Floods of this cold fresh water must have a decided influence on the algal vegetation of pools by lowering the temperature and salt concentration, increasing aeration, and thus making the vegetative conditions more favorable. Subsequent evaporation and the "run-off" from local showers increase the salt content to a maximum and again subject algae to unfavorable vegetative conditions, thus bringing on great reproductive activity. The *Spirogyra* figured in this note was collected in a pool which had gone through a similar cycle of changing conditions.

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[2] WEST, W. and G. S., Observations on the Conjugatae. Ann. Botany **12**:29–58. 1898.

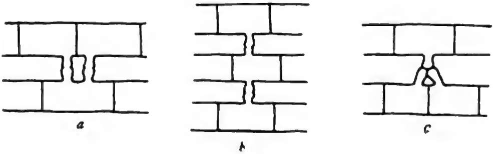

FIG. 3

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BRIEFER ARTICLES

CROSS-CONJUGATION IN SPIROGYRA WEBERI

(WITH ONE FIGURE)

The writer has reported[1] the occurrence of cross-conjugation in *Spirogyra inflata* (Vauch.) Rabh., which was found in material collected in April 1915. In the spring of 1917 another species was collected in cross-conjugation. Glycerine mounts were made and examined. The phenomenon in this case is very similar to that in *S. inflata*. Table I shows the dimensions of *S. inflata* and *S. Weberi* as given by WOLLE and DETONI, also the material collected by the writer in 1915 (which has been identified as *S. inflata*), and that collected in 1917 which corresponds sufficiently with *S. Weberi* to be identified with that species.

TABLE I

	ZYGOTE		ZYGOTE CELL		VEGETATIVE CELL	
	Length	Width	Length	Width	Length	Width
S. inflata*.........	2×W	30–36	Greatly inflated		42–144	14–18
1915 coll.†........	45	25.9	85	34	99.0	15.6
S. Weberi.*.......	2×W	26–30	Slightly inflated		100–350	18–25
1917 coll.†........	62.9	29.6	87.2	35.2	101	25.9

* Dimensions according to WOLLE and DETONI.

† Average of 15 measurements.

Since there is a possibility of considerable variation in the size of a plant owing to various causes, such as food, light, heat, etc., it is probably well to add the fact of the great difference in the inflation of the zygote cells. WOLLE says that the zygote cell of *S. inflata* is greatly inflated, while *S. Weberi* is but slightly inflated. If we establish a ratio by dividing the diameter of the zygote cell (d) by the diameter of the vegetative cell (d'), $\frac{d}{d'}$, and apply it to the material collected in 1915, we get $\frac{d}{d'}=2.205$; while applied to the 1917 material we get $\frac{d}{d'}=1.359$. This shows a remarkable difference between the two collections, and taken with the facts shown in the table leads the writer to identify the 1917 collection as *S. Weberi* Keutz.

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[1] CUNNINGHAM, BERT, Sexuality of filament of *Spirogyra*. BOT. GAZ. 63:486–500. 1917.

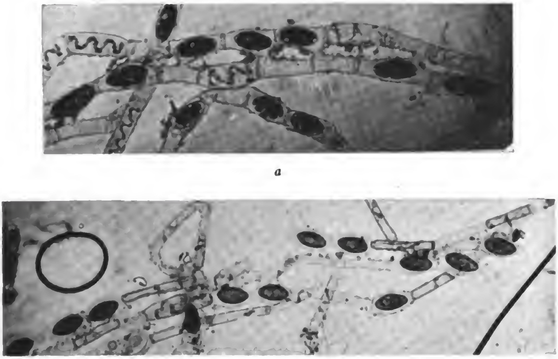

FIG. 1.—*a*, *Spirogyra Weberi*; *b*, *S. inflata*

These differences are shown in fig. 1, from preparations made at the same magnification, in the same mounting media of identical concentration.—BERT CUNNINGHAM, *Trinity College, Durham, N.C.*

AN ENDEMIC BEGONIA OF HAWAII

The flora of the Hawaiian Archipelago exhibits many pronounced peculiarities. Among these the high endemism, nearly 85 per cent of the spermatophytes, is noteworthy and unexcelled. One of the specific instances of endemism, very interesting to the student of plant distribution, is the solitary begonia, *Hillebrandia sandwicensis* Oliver. This lone species, sharply precinctive in its zonal range, is undoubtedly a vestige of an ancient flora more primitive than that which the islands now possess. Its presence in our flora constitutes one of the many evidences, floral, faunal, and geological, that at one time in the history of the

Pacific Basin the Hawaiian Islands were much more closely associated with the Andean and South Pacific regions than they are at present.

The Begoniaceae comprise 4 genera, of which two are monotypic. *Begonia*, with 400–500 species in tropical and subtropical countries, gives the family its name and definition. *Begoniella* has 3 species in Colombia. *Symbegonia* in New Guinea and *Hillebrandia* in Hawaii are monotypic and little known. As BAILEY[1] remarks, "The begonias are exceedingly variable, the genus running into about 60 well-marked sections, but the intergradations are so many and the essential floral characters so constant that it is impracticable to break up the great group into separate genera."

Considering the family as a whole, it is practically absent from the Pacific region. The two great begonia regions are (1) South America along the Andes to Mexico; and (2) the eastern Himalayas southeastward to the Malay Peninsula. With the exception of the two vestigial and little-known species, one in New Guinea and the other in Hawaii, the entire family is now without representation in the far-scattered island groups of the southern, equatorial, and northern Pacific biological provinces.

The genus and species found in Hawaii was described by OLIVER (Trans. Linn. Soc. **25**:361. *pl. 46*). The generic name is in honor of Hawaii's greatest botanist, WILLIAM HILLEBRAND, who resided in the islands for many years, made an exhaustive study of the land flora, and was the author of *Flora of the Hawaiian Islands* (1888). *Hillebrandia* differs from *Begonia* in having the ovary free in its upper third, and in bearing petaloid organs in the female flowers; in all other features it strongly resembles the true begonias.

This beautiful and interesting plant is confined to the montane rain forest zone. It occurs on all the larger islands of the group, with the exception of Hawaii, from which it has not been recorded. Its altitudinal range is from 3000 to 6000 ft. The islands of Kauai and Maui appear to possess this plant in greatest abundance; it is common in the upper levels of the former, and occurs in practically all of the wet ravines of West Maui and Hale-a-ka-la. In the Koolau Gap of Mount Hale-a-ka-la it attains perfection and a height of 6 ft. On the windward precipices of the island of Molokai it forms a beautiful drapery, and is very showy, although the individual plants are not as fine as those which grow in more sheltered localities. On Oahu it is very rare, and is restricted to the upper levels of Mount Ka-ala, and a few spots in the Punaluu Mountains. It is very shade tolerant and is usually found in the vicinity of waterfalls or in the depths of narrow, sunless ravines. In many of its ecological characters it resembles the endemic *Gunnera petaloidea*.

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[1] BAILEY, L. H., Standard cyclopedia of horticulture.

The native Hawaiian name for *Hillebrandia* is *Pua-maka-nui*, literally "the flower with the big eyes," referring to the large, showy flowers, which contrast strongly with the gloom of its habitat. On the island of Kauai it is known as *Ala-aka-awa;* the Kauai natives use many names and words which are used in no other parts of the islands. The rhizomes of many begonias, particularly those of South America, are bitter and astringent, and are used medicinally by the natives of those countries. It does not appear that the primitive Hawaiians used *Hillebrandia* in any way, although it should be stated that much of the medicinal lore of ancient Hawaii has been irrevocably lost.—VAUGHAN MACCAUGHEY, *College of Hawaii, Honolulu.*

SECONDARY PARASITISM IN PHORADENDRON

BROWN'S[1] illustration of *Phoradendron californicum* parasitic on *P. flavescens*[2] has a twofold interest. First, it records a case of secondary parasitism which seems to be very rare indeed. It has never, so far as I am aware, been noted by workers at the Desert Botanical Laboratory, a number of whom have been especially interested in parasitism. For the most part *P. macrophyllum* and *P. californicum* occur on quite different hosts.[3] Second, the case is of interest physiologically, as BROWN suggests, in its relation to osmotic and other physical phenomena. HARRIS and LAWRENCE, in their study of the sap properties of Jamaican montane rain forest Loranthaceae,[4] find that in these forms the sap extracted from the green stems of the leafless species shows lower osmotic concentration than that from the foliar tissues of the leafy forms. Thus in working with 7 species of Loranthaceae they found average values of the freezing point lowering of 1.153°, 1.176°, and 1.177° in the leafless species as compared with 1.305°, 1.347°, 1.400°, and 1.650° in the leaves of the leafy forms. If the same is true of desert Loranthaceae, the relationship between leafless and leafy parasite observed by BROWN is just the reverse of what might be expected if successful parasitism were dependent upon higher osmotic concentration in the tissue fluids of the parasite.

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[1] BROWN, J. G., Mistletoe vs. mistletoe. BOT. GAZ. **65**:193. *fig. 1.* 1918.

[2] This is presumably *P. macrophyllum* Cockerell, the *P. flavescens macrophyllum* of ENGLEMANN and of some subsequent workers, or one of its varieties. The host here, as Professor BROWN has kindly written me, was a *Fraxinus*.

[3] TRELEASE (The genus *Phoradendron*, p. 14, Urbana. 1916) notes that *P. californicum*, while occurring exclusively on angiosperms, belongs to a group, the "Pauciflorae," which with this and one other exception is limited to coniferous hosts.

[4] HARRIS, J. ARTHUR, and LAWRENCE, J. V., On the osmotic pressure of the tissue fluids of Jamaican Loranthaceae parasitic on various hosts. Amer. Jour. Bot. **3**:438–455. 1916.

As pointed out elsewhere, however, the technical difficulties in the comparison of the tissue fluids of the stems and leaves by the methods as yet available for field work are rather great. In the leafless forms there is danger of including a considerable amount of fluids from woody conducting tissue not at all comparable with that of the green tissue which may be taken to be physiologically homologous with the leaf tissue of the leaves of the tree or of the leafy Loranthaceae. Furthermore, such work as has been done on the rather difficult problem of the physicochemical properties of the tissue fluids of desert Loranthaceae[5] is insufficient to show that the osmotic concentration is lower in the leafless desert forms. Furthermore, the concentration of the sap of desert forms seems to vary rather widely, and even if the average concentration of the fluids of *P. californicum* were lower than that of *P. macrophyllum*, it is quite possible that the individual secondary parasite, *P. californicum*, had a higher concentration than its individual *P. macrophyllum* host.[6]

So far as I am aware, the only direct determination of osmotic concentration in primary and secondary parasitism in the Loranthaceae is that by HARRIS and LAWRENCE (*loc. cit.*) on the Jamaican broad-leaved *Phthirusa parvifolia* parasitic upon the leafless *Dendrophthora gracilis*, which is in turn parasitic upon a tree, *Cyrilla racemiflora*. The sap properties stand in the following relationship: *Cyrilla racemiflora*, $\Delta=1.18$, $P=14.2$; *Dendrophthora gracilis* (on *Cyrilla racemiflora*), $\Delta=1.26$, $P=15.2$; *Phthirusa parvifolia* (on *Dendrophthora gracilis*), $\Delta=1.49$, $P=17.9$. Osmotic concentration increases from the host to the primary parasite and from the primary parasite to the secondary one. Note also that the observed secondary parasitism is the *leafy P. parvifolia* with an average depression of 1.347° upon the *leafless D. gracilis* with an average depression of 1.176°.—J. ARTHUR HARRIS, *Cold Spring Harbor, N.Y.*

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[5] HARRIS, J. ARTHUR, On the osmotic concentration of the tissue fluids of desert Loranthaceae. Mem. Torr. Bot. Club 17:307–315. 1918.

[6] I have individual determinations on *P. californicum* which indicate higher concentration than some found in *P. macrophyllum*. The great difficulty of comparing the sap properties of the two forms lies in the fact that, in the neighborhood of Tucson at least, they occur in the main on different hosts and for the most part in slightly different local habitats.

CURRENT LITERATURE

NOTES FOR STUDENTS

Formation and translocation of carbohydrates in plants.—In a series of three papers from the Rothamsted Experimental Station, DAVIS, DAISH, and SAWYER[1, 2, 3] have reported the results of an investigation designed to test the validity of BROWN and MORRIS' conclusion that cane sugar is the primary photosynthetic product in foliage leaves, that the dextrose and levulose present are products of its hydrolysis, not its precursors, and that levulose is found in excess in the leaves and leaf stalks for the reason that dextrose is more readily utilized in respiration. The introductory review of literature presents an account of work done in this field since the appearance of the memoir by BROWN and MORRIS in 1893. The workers who have given attention to the subject since that time fall into three groups: WENT, STROHMER, STEPHANI, PEKLO, and PARKIN, who adhere to the view that saccharose is the first sugar formed in photosynthesis; MAQUENNE, STRAKOSCH, ROBERTSON, IRVINE and DOBSON, GUTZEIT, and DELEANO, who consider that hexoses are the primary product; and PELLET and COLIN, who hold the belief that saccharose, dextrose, and levulose are formed simultaneously in the leaf and transported as such to the storage organs, where conversion of the reducing sugars into saccharose subsequently occurs.

The authors made analyses of leaves, midribs, and upper and lower halves of petioles of Yellow Globe mangold at three stages of growth: an early stage (August 26) when leaf formation was predominant, the seeds having been sown June 9; an intermediate stage (September 10) when leaf growth had practically ceased and storage of sugar in the root had attained its maximum rate; and a final stage (October 11) when growth of roots had been practically completed. Samples were collected at intervals of 2 hours over a 24 hour period on each

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[1] DAVIS, WILLIAM A., DAISH, ARTHUR JOHN, and SAWYER, GEORGE CONWORTH, Studies of the formation and translocation of carbohydrates in plants. I. The carbohydrate of the mangold leaf. Jour. Agric. Sci. 7:255–326. 1916.

[2] DAVIS, WILLIAM A., Studies of the formation and translocation of carbohydrates in plants. II. The dextrose-levulose ratio in the mangold. Jour. Agric. Sci. 7: 327–351. 1916.

[3] DAVIS, WILLIAM A., and SAWYER, GEORGE CONWORTH, Studies of the formation and translocation of carbohydrates in plants. III. The carbohydrates of the leaf and leaf stalks of the potato. The mechanism of degradation of starch in the potato. Jour. Agric. Sci. 7:352–384. 1916.

of the dates given. Chemical changes subsequent to collection were prevented by dropping the material immediately into a large volume of boiling 95 per cent alcohol containing 1 per cent concentrated ammonia, which instantly destroys the enzymes present. In the subsequent analyses, the methods outlined by the authors in their papers on the estimation of carbohydrates in plant material were employed; the chief new features of these methods are the employment of 10 per cent citric acid for the inversion of saccharose, the estimation of maltose by fermentation with maltase-free yeasts, and the determination of starch by the use of taka-diastase.

Maltose and starch were entirely absent from the leaves at all times, day and night, in all three series. Starch is present in very young leaves, but disappears as soon as the roots have grown sufficiently to be capable of storing sugar. In the first series, hexoses began to increase immediately after sunrise, attained a maximum of 2.16 per cent between 10 A.M. and noon, declined sharply until 4 P.M., then decreased steadily throughout the night to start upward again at 4 A.M. The curve representing saccharose rose more slowly from sunrise, maintaining a maximum of 3.11 to 3.06 per cent from noon to 4 P.M., then dropped in an almost straight line through the night to start up at 4 A.M. Both curves roughly paralleled the temperature curve.

In the second series (that of September 10) both curves were complicated; that for hexose shows a minimum at 8 A.M., with a rapid rise to 7.5 per cent at 1 P.M., followed by a slight decline for 3 hours which is succeeded by a rise to 8.9 per cent at 6 P.M. Two hours later this has fallen to 6.75 per cent, but there is again a rise to a new but lower maximum of 7.81 per cent at 2 A.M., after which there is a sharp decline, continuing until sunrise. The curve for saccharose is similar, in that it shows two maxima at 6 P.M. and 2 A.M., but differs in that the second is much the largest, the amounts being 6.39 and 8.27 per cent. The curves for hexose and saccharose in the third series are alike in that each presents three maxima; for hexose these occur at 1 P.M., 9 P.M., and 3 A.M., the last being greatest, while those for saccharose occur at 3 P.M., 9 P.M., and 3 A.M., the second being considerably higher than the others. In neither the second nor the third series is there any resemblance to the temperature curve. In the first series, the amount of saccharose present is at all times much greater than that of hexose, becoming 7 times as great at 4 A.M., and the fluctuations in amount of hexoses are much greater than those of saccharose. In the second series, hexoses vary between 8.9 and 5.4 per cent and are larger in amount than saccharose, which varies from 8.27 to 4.24 per cent. To this statement there is one exception at 2 A.M., at which hour saccharose is slightly in excess. In the third series, hexoses are again in excess, varying from 12.41 to 9.39 per cent, while saccharose ranges between 9.52 and 4.98 per cent. The variations in saccharose are greater than those in dextrose in both second and third series, and are greater in the third than in the second. Consequently, while the ratio of invert sugar to cane sugar varies, in the first series, between 0.133 (at 4 A.M.) and 0.710 (at 10 A.M.), and is expressed by a curve closely paralleling the temperature curve, the ratio for the second series has a maximum of 1.60 at 4 P.M. and exceeds unity at all hours except at 2 A.M., when it drops to 0.94, but still roughly parallels the temperature curve. In the final series the ratio ranges between 1.93 at 7 A.M. and 1.14 at 3 P.M. as extremes.

For total sugars (hexoses plus saccharoses) the maximum in the August 26 series is 5.26 per cent, reached at 12 noon; the minimum, 1.70 per cent, is attained at 4 A.M.. On September 11 the maximum of 16.08 per cent is attained at 4 A.M., the minimum of 9.98 per cent at 8 A.M., with a second rise to 15.29 per cent at 6 P.M. On October 11 the maximum of 20.99 per cent occurs at 7 P.M., is followed by a slightly lower maximum at 3 A.M., with the minimum, 14.5 per cent, occurring at 7 A.M.

In the first series, pentoses vary during the daylight hours only between 0.37 and 0.45 per cent, dropping again to 0.36 at 8 P.M., only to rise slowly through the night to 0.52 at 4 A.M. Pentosans remain practically constant through the day in the neighborhood of 5.5 per cent, with a maximum of 5.96 at 4 P.M. In the second series, the fluctuations in pentose have much wider limits; there is increase from 0.34 to 0.68 per cent between 10 A.M. and 2 P.M., followed by a fall to 0.45 at sunset and a subsequent rapid rise to 0.71, remaining stationary through the dark hours and dropping suddenly to 0.5 at 4 A.M. Pentosans rise slightly between noon and 2 P.M., then remain stationary until 4 A.M., when there is a second slight rise, but the fluctuations are between 4.42 and 5.9 per cent as extremes. In the final series, pentoses remain almost unchanged at 0.9 per cent from 9 A.M. until 9 P.M., declining to a minimum of 0.61 per cent at sunrise (7 A.M.). Pentosans here show very slight fluctuations, but are slightly higher (6.77 to 7.15 per cent) during darkness than in the day (6.21 to 6.55 per cent). The total percentage of material soluble in alcohol falls slowly throughout the day in the first series, attaining a minimum at 4 P.M., then remains nearly constant through the night. In the second series there is a decline in alcohol-soluble constituents from 4 A.M. to 1 P.M., then a rise continuing until sunset, with a drop between 6 and 8 P.M., then a very slow rise from 47.2 to 51.3 per cent between 8 P.M. and 4 A.M. In the third series the percentages of alcohol-soluble materials are almost constant from 7 A.M. to 9 P.M., varying only from 52.0 to 54.9 per cent, then run down at 11 P.M. to 47.9 per cent, only to return at the next sampling to the general level.

The increases in pentosans throughout the day in the first and second series are attributed in part to the building of new ligneous tissue, in part to the formation of gums which play the rôle of reserves. In the third series, when the leaves have ceased to grow, the fluctuations are apparent rather than real, being due to fluctuations in total sugars. The striking feature of the curves for sugar are the two night maxima which occur in both second and third series, since both hexoses and saccharose increase synchronously to a point higher than that reached during insolation, their sum total also exceeding that attained in the day and reaching its greatest amount at the same time, between midnight and 3 A.M, in both series, so that the results cannot be due to interconversion.

In the entire absence of both maltose and starch, the authors attribute this increase to the conversion into saccharose and invert sugar of some gummy substance, which is present in large amounts and which is precipitated in semicrystalline form by basic lead acetate after treatment with taka-diastase. There is also an interconnection between the fall and rise of pentoses which occurs between 4 and 8 P.M., and the change in the opposite direction in saccharose and hexoses.

While pentosans make up 8.58 to 9.61 per cent of the insoluble matter of the leaves in the first series, there is an increase to 9.83–10.85 per cent in the second and a further increase to 13.70–15.35 in the third. While in the first series about one-half the saccharose and nearly all the hexoses are used up during the night, the second and third series show a very much larger amount of reducing sugars present at the beginning of the day, and the amount of these up to the attainment of the first maximum is always greater than that of saccharose, but when root growth is nearly complete, as in the third series, the range of variation in cane sugar in the leaf becomes much greater, the leaf apparently acting as a storage reservoir during insolation. The range of variations during growth is summarized as follows:

Series and date	Insoluble in alcohol	Saccharose	Hexoses
I, August 26........	57.5–62.9	1.50–3.11	0.20– 2.16
II, September 10....	45.3	4.24–8.27	5.38– 8.90
III, October 11.....	55.8	4.98–9.52	9.39–12.41

	Pentose	Pentosans	Ratio, invert to saccharose	Total saccharose plus hexose
I, August 26.......	0.36–0.52	5.19–5.96	0.13– .71	1.70– 5.20
II, September 10....	0.34–0.76	4.42–5.90	0.94–1.60	9.98–16.08
III, October 11.....	0.61–0.92	6.21–7.15	1.14–1.93	14.50–20.99

Information as to the translocation of the sugars was obtained by making separate analyses of the midribs and petioles. At any given picking the amount of sugars and alcohol soluble matter is always greater in midribs than in leaves, greater in top halves of petioles than in midribs, and greater in lower halves than in top halves of petioles. In the first series, the total amount of hexoses and of apparent levulose in the stalks increases very rapidly during the forenoon to reach a maximum at noon, while the corresponding increases in dextrose and saccharose are extremely slight, dextrose being actually larger in amount at midnight than at any time during the day. In the bottom halves of the petioles of the series, total hexose, apparent dextrose, and apparent levulose run very closely together, reaching a maximum at noon, declining steadily to midnight, and then separating, as levulose continues to decline while the others start upward again. Saccharose rises slightly from 6 A.M. to noon, and then remains stationary for the succeeding 18 hours. In the second series, in which top and bottom halves of petioles were not analyzed separately, saccharose was constant throughout the 24 hours; total hexoses and apparent levulose were least at 11 P.M., increased slowly to 4 A.M., then more rapidly until 4 P.M., when they again declined together until 11 P.M. Apparent dextrose rose from 4 A.M. until 4 P.M., then remained stationary throughout afternoon and night. In the midribs, however, total hexoses decreased slowly from 10 A.M. to 4 P.M., then more rapidly through the night, rising again at 4 A.M. Apparent levulose decreased, apparent dextrose increased, from 10 A.M. to 4 P.M., after which dextrose rather rapidly fell off while levulose slowly increased until 4 A.M., when both began to increase. Saccharose was stationary from 10 A.M. to 4 P.M., then increased slowly and uniformly through the evening and night, beginning to fall at 4 A.M. There is, therefore, a steady movement of sugars from leaves to midribs, thence through the stalks, the maximum in leaves at 2 A.M. moving onward into the stalks to give a maximum there at 6 A.M., which is succeeded by a minimum 4 hours later, when a large part of the sugar formed during the insolation of the preceding day has passed from stalk to root. The ratios of invert sugar to cane sugar at any given hour of the day, as at 6 A.M., September 10, when it is 1.48 in leaf, 3.32 in midrib, and 5.27 in stalk, are significant, showing as they do that there are progressively more and more hexoses in the stream of sugars as it passes from leaf to root. On August 26 the stalks had at noon 4.25 per cent saccharose and 11.57 per cent hexose; at 10 A.M., September 10, 4.82 per cent saccharose and 20.5 per cent hexose; and at 11 A.M., October 11, 5.29 per cent saccharose and 25.7 per cent hexose. This is strong evidence that hexoses are translocation forms produced by the conversion of cane sugar, as is the fact that cane sugar greatly predominates in the leaves in the early stages of growth, prior to the beginning of storage in the roots. Further evidence is seen in the fact that cane sugar is the predominant sugar in the leaves of the potato, vine, and snowdrop, although these plants store carbohydrate as starch, dextrose, and inulin respectively, and do not store cane sugar. Cane sugar is therefore formed in the mesophyll, transported into the vessels, undergoes progressive inversion as it passes onward through midribs and stalks, enters the roots as reducing sugars, and these are there transformed once more into saccharose. The authors have not studied the mechanism of this synthesis in the root; invertase was shown to be present in the sieve tubes but was not found in roots by ROBERTSON, IRVINE, and DOBSON, and it is believed to be the agent in the inversion occurring during transport. Since the existence of the saccharogenic enzyme of BORDET has not yet been substantiated, and the probability ot reversible zymohydrolysis by invertase is contra-indicated by the absence of invertase from the roots, the authors are unable to formulate a theory as to the agent responsible for this synthesis.

In the second paper of the series DAVIS reports the result of a study of the dextrose-levulose ratio in the mangold. The determination of these sugars by polarimetric methods is falsified by the presence of optically active substances not precipitable by basic lead acetate. Glutamine, glutaminic acid, and aspartic acid give a dextro-rotation which is increased by acids, while asparagine gives either dextro- or laevo-rotation accordingly as the solution is or is not acid. In the mangold and sugar beet there is an apparent excess of dextrose over levulose which is due to the presence of glutamine, while in snowdrop, tropaeolum, and potato the presence of asparagine results in an apparent excess of levulose. In the first case the apparent excess of dextrose increases progressively from leaves through midribs and stalks as a consequence of the transfer of the impurity; in the leaves the dextrose-levulose ratio is in the neighborhood of unity; in the midribs and stalks it ranges from 2.5 to 10.0. The pentoses which are present in the alcoholic extract also affect the readings.

The author determined the proportions of the two sugars present in the three series discussed in the preceding paper, using the methods there employed. In the early morning there was found in young leaves a dextro-rotation still greater than that which would be observed if all the sugar present were dextrose. In older leaves there appeared to be a steady formation of a laevo-rotatory substance and a gradual transformation into a compound having still greater laevo-rotation. The author considers that this is manufacture of asparagine and transformation into aspartic acid. Both in the second and the third series there are three rises and three falls in the amount of apparent dextrose in 24 hours, this fact pointing to a regular and rhythmical variation in the rate of production of the optically active impurities.

The character of the optically active impurities in the upper portions of the stalks is quite different from that in the lower portions, as shown by the fact that when determinations of the sugars in the lower portions of the stalks are made simultaneously by polarization and reduction methods the polarization results are 40 per cent higher than those obtained by reduction, while on the upper portion of the same stalks the results by polarization are 85 per cent lower than the reduction figures. Hence the optically active substances interfering with the polarization are quite different in the two portions of the stalk, suggesting the optical behavior of d- and l-asparagine and d- and l-glutamine. Furthermore, there are two different optically active substances at different times during the 24 hours. For all these reasons we can at present obtain no true values for these sugars, and there is at least nothing to disprove the assumption that dextrose and levulose exist in the leaves and stalks as invert sugar, travel in approximately equal amounts to the roots, and there undergo recombination into saccharose.

In the third paper of the series **DAVIS** and **SAWYER** have applied similar methods of study to the potato as a typical plant forming starch in the leaves, paying especial attention to the mechanism of degradation of starch in the leaf, and have extended the study to a considerable number of plants, including turnip, sunflower, dahlia, carrot, grape, and others. They were able to find no maltose at any time, either during day or night, in plants storing much starch in the leaves, although more than 500 analyses by means of maltase-free yeasts were made. Hence the authors consider that **BROWN** and **MORRIS** were incorrect in their conclusion that diastatic formation of maltose and transfer as such occurs in the case of the leaf of *Tropaeolum*. **Brown** and **Morris** unquestionably had maltose present, as shown by the fact that they obtained the osazone and that there was an increase in the reduction of copper after treatment with maltase, but the authors consider that this result may be explained by the fact that the material used by **Brown** and **Morris** was subjected to preliminary drying in an oven. They regard the leaf as having a mixture of enzymes analogous to that found in *Aspergillus oryzae*, and that it is therefore able to split maltose rapidly and completely to dextrose. They destroyed all enzymes instantly by dropping the leaves as they were picked into a mixture of boiling alcohol and ammonia. As maltase is easily destroyed by heating to 55°, it was first to go out of action in **Brown** and **Morris'** oven-dried material, while other more heat-resistant enzymes went on forming maltose which was not split up, hence was found in the analysis. This hypothesis is borne out by the results; **Davis** and **Sawyer** invariably found more starch in the leaves than did **Brown** and **Morris**, the amount always exceeding the sum of starch plus maltose found by the last-named authors. **Kluyver** employed a biochemical method, using *Torula monosa* to ferment the hexoses only, *T. dattilla* to ferment the cane sugar and hexoses, leaving maltose, and found very small amounts of maltose.

The authors consequently believe that starch degradation goes immediately down to hexoses with no stop at maltose; that plants must reduce sugars to this form before they can be utilized; and that the fact that the sugar in leaf stalks is largely hexose is thus explained, as is the presence of invertase in almost all plant parts. **Daish** found maltase wherever starch is found in leaves, but believes it to be an intracellular enzyme occurring in close proximity to diastase, hence never found in the vessels of the stalks.

In the leaf saccharose is always greatly in excess of hexoses; in the stalks the reverse is always true. Hence saccharose must be the first product of photosynthesis and hexose a translocation form. The authors are led by unpublished work with a variety of other plants, such as sunflower, grape, and snowdrop, to the conclusion that this is the general situation with all plants regardless of the form in which final storage may occur. Like the potato, the plants just mentioned have two optically active impurities which are formed at different periods in the 24 hours, and hence have apparent large fluctuations in the dextrose-levulose ratio, which it is impossible to measure correctly by reason of their presence.

The authors found in the leaves considerable amounts of dextro-rotatory, water-soluble material which was not soluble starch or dextrin, which was greatest in amount between 4 and 8 P.M. Its period of greatest formation synchronizes with the high tide of saccharose and the period of most rapid starch formation, hence it seems to be intermediate between the hexoses and true starch. Starch is very rapidly reduced after sunset, then more slowly with the hexoses rising, while the starch rises again at dawn considerably before the hexoses show increase. The curves for hexose, starch, and this dextrorotatory material are intimately related and indicate interconvertibility; the last-named substance may be a protein or a gum standing in causal relation to starch synthesis.

In the leaves the daily fluctuations of alcohol-soluble substances is through a range almost twice as great as that of total sugars. In the stalks the same is true, in which respect the potato is unlike the mangold. The dextrose-levulose ratio determinations are of little significance because of the presence of laevorotatory non-sugars, probably asparagine, but the authors regard them as being present in equal amounts as splitting products of saccharose. The polarization readings for saccharose were aberrant as in the mangold, by reason of the presence of impurities of the same character. Levulose apparently predominates in the leaves and dextrose in the stalks, by reason of the accumulation of dextro-rotatory stuffs in the latter, or possibly by reason of an actual excess due to the using up of levulose in tissue building. That this latter alternative is the correct one is indicated by the fact that the determinations of cane sugar by polarization and by reduction are in close agreement.—JOSEPH S. CALDWELL.

The Oenothera situation.—Three recent papers have cast some light on the perplexing *Oenothera* situation. One of the most serious objections to the mutation theory has been that mutants which have appeared under observation in artificial cultures have regularly been interfertile, while incipient species in nature are essentially intersterile. METZ and BRIDGES[4] have shown that mutants may be intersterile, describing two cases in *Drosophila*, each involving two mutants that either refuse to cross or else give sterile hybrids.

MULLER[5] has explained a curious case in *Drosophila*, which strikingly resembles the *Oenothera* situation. A certain race of *Drosophila* breeds practically true, and yet it is in a heterozygous condition. This paradox is explained by "balanced lethal factors," a given chromosome and its allelomorph each carrying lethal factors. When one of these factors is present in a zygote it brings death, but when both factors are present they are antagonistic in their action and the zygote develops into a mature individual. Thus the homozygotes, which are thrown off every generation, die in infancy, since they contain single lethal factors; only the heterozygotes survive, for in them alone are the lethal factors balanced and inactive. The result is that the heterozygous race seems to breed true. This balanced race, as we should expect, gives in crosses twin hybrids as in *Oenothera* crosses, while crossing two such balanced races in *Drosophila* gives multiple hybrids, as also occurs in *Oenothera*.

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[4] METZ, C. W., and BRIDGES, C. B., Incompatibility of mutant races in *Drosophila*. Proc. Nat. Acad. Sci. **3**:673–678. 1917.

[5] MULLER, HERMANN J., An *Oenothera*-like case in *Drosophila*. Proc. Nat. Acad. Sci. **3**:619–626. 1917.

Another similarity with the *Oenothera* situation is that in this *Drosophila* race there would occasionally appear recessive mutants on one of these two "lethal chromosomes." These recessive mutants, however, could not become manifest on account of the enforced heterozygosity. They could only become manifest when crossing over occurred and homozygosity was thus made possible. "As crossing over occurs with predictable frequencies, those individuals showing characters abnormal to the stock were thrown continually in a definite, very small percentage of cases." In just such a regular, although small, percentage of cases does *Oenothera Lamarckiana* throw its mutants. MULLER concludes that the *Oenothera* situation is to be explained by a similar mechanism, "but probably the lethal effect in *Oenothera* is on the gametes rather than on the zygote."

A similar idea appears in a paper by DAVIS,[6] in which we find summarized some of the evidence, old and new, on the suspected hybrid condition of *Oenothera Lamarckiana*. The regularity with which the same old mutants are thrown and the production of twin hybrids in crosses suggest to this author the hybrid condition of *O. Lamarckiana*. The facts that about one-half of both pollen and ovules, in random distribution, are sterile, and that only 30–40 per cent of the seeds produced are fertile, suggest that only such gametes and zygotes are fertile as will reproduce the hybrid type. The argument is essentially similar to that of MULLER. "If it could be shown that in every group of 4 pollen grains (tetrad) formed as the result of the reduction mitoses only 2 grains are perfect, the conclusion would be justified that pollen sterility was the result of this segregation division." The author regards this as impossible, however, since abortion takes place after the tetrads have lost their identity. On this point we may quote from a review which appeared in this journal[7] on some work of GEERTS. "In *Oenothera Lamarckiana* 50 per cent of the ovules are found to degenerate and about 50 per cent of the pollen grains, *two from each tetrad of spores*."

It begins to look more and more probable that our classic illustration of mutation is really about the most unfavorable material that could have been chosen for the subject, owing to its germinal complexities. This complexity and seeming lack of conformity have served to make "*Oenothera* genetics" a science in itself. Geneticists will feel relieved when these data on *Oenothera* are finally interpreted by the Mendelian system, and there is now much hope that this may soon come to pass.—MERLE C. COULTER.

Edible and poisonous mushrooms.—Popular interest in the fleshy fungi appears to be growing in many sections of the country. This interest may be attributed to several different causes, chief of which are to be found in the availability of these plants as subjects for nature study and in the desire to add to the dietary a wholesome and palatable food growing without cultivation in forest and field. Here it is almost totally wasted as an article of food, because the comparatively small number of poisonous species cannot be distinguished from the many edible ones, for lack of the elementary knowledge necessary to recognize the more common forms. For this reason, and particularly at this time when there is a worthy desire to conserve every available item of food, nutritious or appetizing, it is gratifying that public institutions devoted to research and to the dissemination of useful information are recognizing the growing demand for popular instruction in the identification of edible and poisonous mushrooms.

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[6] DAVIS, B. M., A criticism of the evidence for the mutation theory of DE VRIES from the behavior of species of *Oenothera* in crosses and in selfed lines. Proc. Nat. Acad. Sci. **3**:704–710. 1917.

[7] BOT. GAZ. **47**:481. 1909.

One of the most recent pamphlets devoted to this subject is from the Illinois State Laboratory of Natural History.[8] There is an introductory chapter treating in a simple and clear manner of the nature, structure, life-history, ecology, etc., of the fleshy fungi, with a few suggestions as to their collection and preparation for the table. Between 50 and 60 species are described and illustrated by photographs. The arrangement of descriptive text and illustrations is such as to make the work very convenient for practical use by the amateur, and it is to be hoped that the effort of the author will succeed in still further stimulating interest in this group of fungi, often despised under the name of "musheroons," and in leading its users to the desired knowledge of a satisfactory number of edible and poisonous kinds. Following the introductory chapter, two pages generally are devoted to a single species, one page to the descriptive text, and the opposite page to the photograph. As one reads the text the eye easily turns to the photograph in which most of the specific features can be verified.

The photographs are in general good, for many of the specific as well as the generic characters are brought out in detail. To the reviewer, however, they seem to lack the finish and excellence which should be obtained from these plants. Whether this is due in all cases to a lack of care in the original photographs, or to faulty reproduction, is uncertain. The background in a number of cases is unnecessarily spotted, and in general the photographs appear "flat" and not well shaded. It is perhaps a matter of taste in which there may be reasonable differences of opinion, but it would appear preferable that the scale in the photograph should not occupy such an obtrusive position as it does in covering up parts of the plants, when it would serve as good a purpose if placed by the side.

It appears that a few of the plants are not correctly named. For example, pl. 137 does not appear to be *Clavaria cristata;* pl. 119 is probably all *Craterellus cantharellus;* pl. 113 does not resemble *Pholiota squarrosa*, but rather a *Hypholoma*, related to or identical with *H. lachrymabundum*. The omission of *Amanita* "*muscaria*", a very poisonous species of wide distribution, should be noted. —GEO. F. ATKINSON.

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[8] McDOUGALL, W. B., Some edible and poisonous mushrooms. Ill. State Lab. Nat. Hist. Bull. 11:413–551. *pls. 85–143.* 1917.

Economic importance of diatoms.—MANN[9] gives an interesting discussion of the uses of diatoms. Among these he enumerates the use of fossil diatoms as abrasives in polishing powders, tooth powders, etc. They have also been used as a food adulterant by mixing with flour, thus increasing the bulk of food but adding nothing to its nutritive value. They were used in this way by the "Earth Eaters." A later similar use was as an adulterant of candy, but this use is now prohibited by law. They were also formerly used as an absorbent of nitro-glycerine in the manufacture of dynamite. There are beds of diatomite several hundred feet thick on the Pacific coast, and the use of them as a substitute for asbestos in packing steam pipes, as filler for refrigerators, and in the manufacture of pottery is increasing. Another new use in medicine is as a filter for serums. It is suggested that their beautiful designs be used as patterns in the ornamentation of jewelry, wall paper, etc.

Since diatoms store their food in the form of oil instead of starch, it is believed that they have been one of the sources of petroleum. On account of their being so minute that living ones may be carried great distances in the ocean, they may be of use in determining the direction of ocean currents. One argument that supports NANSEN's theory that there is a current passing northward from Behring Strait across the north polar regions and down the coast of Greenland and Norway is that the diatoms of these localities are of similar species. Perhaps the one use that is of supreme importance is the furnishing of food either directly or indirectly for aquatic animals. Diatoms are chlorophyll-bearing plants, and are the greatest agency in the water for changing inorganic into organic matter, hence a knowledge of diatoms is fundamental to a study of the food supply of fish and other aquatic animals. Animal life is very abundant on the shores of the Antarctic continent, and in that region there is very little land vegetation. The greater part of the food for all of these animals is supplied originally by the diatoms.

The statement that EHRENBERG estimated the number of individuals in a cubic inch of diatomite at 40,000,000 should be 40,000,000,000. The statement is made that diatoms are so minute that 100 of them could be placed on the head of a pin. This is well within the facts, for that number of the smallest could find room on the point of a pin. The use mentioned of the diatoms *Pleurosigma angulatum* and *Amphipleura pellucida* as test objects for microscope objectives has been discontinued. The Bausch and Lomb Company state that the "Abbe test plate" is now used entirely and is more accurate and reliable.—C. J. ELMORE.

Addisonia.—The second number of the second volume of this finely illustrated series, issued June 30, contains colored plates and popular descriptions of *Solidago juncea, Echeveria multicaulis, Catasetum viridiflavum, Sagittaria latifolia, Baccharis halimifolia, Xanthisma texanum, Secum Bourgaei, Cimicifuga simplex, Feijoa Sellowianus*, and *Aster amethystinus*.

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[9] MANN, ALBERT, The economic importance of the diatoms. Smiths. Rep. 1916: 377–386. *pls. 1–3.* 1917.

The first number of the third volume of this journal, published by the New York Botanical Garden, contains colored plates and popular descriptions of *Anonia atropurpurea* (Eastern North America), *Aster novaeangliae* (United States and Canada), *Gymnocalycium multiflorum* and *G. Mostii* (Argentina), *Euonymus alata* (Eastern Asia), *Diospyros virginiana* (Eastern United States), *Lepadena marginata* (Central and Western United States), *Maackia amurensis Buergeri* (Japan), *Hibiscus oculiroscus* (Eastern United States), *Cornus officinalis* (Japan), *Opuntia lasiacantha* (Mexico).—J. M. C.

Morphology of wheat.—JENSEN[10] has investigated certain strains of wheat and the result is perhaps our fullest account of the morphology of this important plant. The subjects considered are development of spike and flower, of microspore and male gametophyte, of megaspore and female gemetophyte, fertilization and development of embryo, and endosperm. An interesting record is that fertilization occurred from 32 to 40 hours after pollination.—J. M. C.

Intrafascicular cambium in monocotyledons.—Mrs. ARBER[11] has added to her previous observations[12] of intrafascicular cambium in monocotyledons other observations which include Araceae, Dioscoreaceae, Iridaceae, and Potamogetonaceae. Such cambium is now known to occur in "all but two of the cohorts into which ENGLER divides the monocotyledons; the exceptions are the Triuridales and the Synanthae."—J. M. C.

Seed position and growth.—It has been found that bean seeds planted with the eye up give a somewhat lower degree of germination and growth than when the seed lies flat or is placed eye down.[13] This seems to show that the common practice of dropping seeds flat upon the soil when planting gives results that are satisfactory.—GEO. D. FULLER.

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[10] JENSEN, G. H., Studies on the morphology of wheat. Bull. 150, State Coll. Washington. pp. 21. *pls. 5.* 1918.

[11] ARBER, AGNES, Further notes on intrafascicular cambium in monocotyledons. Ann. Botany **32**:87–89. *figs. 4.* 1918.

[12] BOT. GAZ. **64**:350. 1917.

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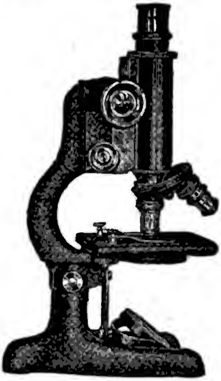

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THE
BOTANICAL GAZETTE

Editor: JOHN M. COULTER

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A CONTRIBUTION TO THE LIFE HISTORY OF IMPATIENS SULTANI

ALICE M. OTTLEY

(WITH PLATES XIV, XV)

This paper is based upon a study of slides made through a series of years for class use in the Botany Department of Wellesley College. The material was taken from greenhouse plants of the rose or bright pink variety of *Impatiens Sultani* Hook. The bright red and light pink varieties also were growing in the greenhouse, but care was taken to collect material from the rose-flowered plants only. Some of the plants from which the flowers were collected were chance seedlings. No attempt was made to determine whether or not these were a pure strain of the rose-colored form. In BAILEY's (4) *Standard Cyclopedia of Horticulture* the original form of *I. Sultani* is given as a rich scarlet, shades ranging from pink to almost purple being found on hybrids or sports. If this be true, then all the rose-colored forms used for this study are either hybrids or sports.

According to BAILEY the species *I. Sultani* was originally found in Zanzibar and named by HOOKER in honor of the Sultan of Zanzibar. In ENGLER and PRANTL's *Die Natürlichen Pflanzenfamilien* (**16**) it is cited from Sierra Leone, Western Africa. It is stated in GRAY's *Manual* that the Balsaminaceae often contain two kinds of flowers, the large showy ones which rarely ripen seeds, and small ones which are cleistogamous. *I. Sultani* is not given by ENGLER and PRANTL in their list of species containing cleistogamous flowers, and I was unable to find any cleistogamous flowers on the many plants of this species which were investigated.

The material fixed ranged from very small buds to young fruits. In preparing the buds for fixing, the smallest ones were put up entire; the sepals and petals were removed from all others; and in the largest buds the pistil and stamens were separated. From the flowers and the fruit only the ovaries were preserved and these were trimmed slightly at the angles to allow more rapid penetration of the fixer, which in all cases was Flemming's chromo-acetic solution. In general, the material was sectioned longitudinally and stained with Flemming's triple stain.

Ovary

The ovary consists of 5 carpels with axial placentation. There are several ovules in each loculus and the age of the ovules in a given loculus advances from base to apex, the youngest being at the base of the ovary. At the time when the microspore mother cells are in prophase of the heterotypic division the ovules appear as slightly curving outgrowths from the placenta, with or without any indication of the inner integument (fig. 1). It is apparent that the ovules of *I. Sultani* occur earlier in relation to the development of the anthers than is the case in many other plants. Miss BLISS (**8**) reports that in *Viola* the ovule initials cannot be detected when the microspore mother cells are in the prophase of the heterotypic division, and similar observations have been made by many other investigators.

As the inner integument begins to appear, a single hypodermal archesporial cell becomes differentiated at the apex of the nucellus (fig. 2). *I. Sultani* agrees with *I. pallida* (Miss RAITT **37**) in having but the one archesporial cell, but differs from that species in having no parietal cell cut off from the archesporial cell. According to COULTER and CHAMBERLAIN (**15**) there is a general tendency to suppress the parietal tissue among monocotyledons and Archichlamydeae. "The suppression of parietal tissue among Archichlamydeae is most extensively displayed by the Ranunculaceae and its allies rather than by the more specialized groups." Balsaminaceae, one of the higher groups of the Archichlamydeae, shows complete suppression of parietal tissue in *I. Sultani;* in *I. pallida*, however, Miss RAITT (**37**) describes a parietal cell, but her illustrations are not very conclusive.

From the first the megaspore mother cell is the only hypodermal cell at the apex of the ovule. It is surrounded by the epidermis of the nucellus at its sides and apex, and is bounded by several nucellar cells at its base (fig. 2). The cell is slightly longer than wide and extends almost to the plane of insertion of the inner integument. It keeps pace with the growth of the ovule and continues to occupy all of the nucellus within the epidermis except in the chalazal region. As growth continues it changes from a broad cell to a long narrow one (figs. 2-4, 6).

The nucleus of the megaspore mother cell contains one nucleolus which at first is separated from the chromatic network by a clear area (fig. 2). As division is initiated, the chromatic reticulum forms a more or less complete spirem, separates from the nuclear membrane, collects about the nucleolus, and enters the synaptic stage (figs. 3, 4). On recovery from synapsis the spirem spreads out into the nuclear cavity and very soon exhibits the second contraction stage (fig. 5) similar to that which has been described for *Lilium* and several other angiosperms by ALLEN (**2**), MOTTIER (**32**), and others. According to OVERTON (**35**), this phenomenon does not occur among the majority of the angiosperms.

During this stage the spirem is thick, and at places uneven and massed. Here and there, in the less condensed areas, light streaks show, suggesting either a longitudinal splitting of a single spirem or an approximation of two. The contracted spirem is in contact with the nuclear membrane at several points, but the greater amount of the chromatic material is near the nucleolus at the center of the nucleus. At this time the nucleus is near the micropylar end of the megaspore mother cell. About midway between it and the chalazal end are numerous fibers with blue staining dots scattered among them. This characteristic has been observed in several megaspore mother cells, but its significance was not determined. These fibers played no apparent rôle in the formation of the spindle or in the development of the cell wall, since they disappear before the first division. However, they may represent an early assembling of the kinoplasmic substance preparatory to spindle formation.

Fig. 6 shows the spirem partially segmented with the nucleolus near the center of the cavity and the segments projecting in from the nuclear membrane. Later the chromosomes become very short and group themselves about the nucleolus (fig. 7). At this time they suggest the tetrads described for many animals and closely resemble those of *Arisaema triphyllum* as figured by ATKINSON (**3**). A typical bipolar spindle is formed and the bivalent chromosomes when arranged at the equatorial plate appear as very short X's, V's, and Y's.

Two cells separated by a distinct cell wall result from the heterotypic division and form the axial row (fig. 8). The micropylar cell of this row is smaller than the other, and disintegrates very quickly. The chalazal cell grows and is the mother of the embryo sac. An axial row of two cells is not common among the Archichlamydeae. TREUB (**43**) describes an axial row of two cells for *Viscum articulatum*, and several cases have been reported among the monocotyledons. Miss RAITT (**37**) states that 4 megaspores are formed in *I. pallida*, but makes no sketch showing them. In her fig. 1, *J*, she shows an ovule containing a large cell which she names the functional megaspore. Between it and the epidermis a small disintegrating cell appears. The sketch closely resembles the appearance of the ovules of *I. Sultani* with an axial row of 2 cells and throws doubt upon her assertion that there is an axial row of 4 cells.

The micropylar cell of the axial row is never large, and is so short-lived that it is easily overlooked, and the embryo sac seems to arise directly from the megaspore mother cell, as in *Lilium*. As the micropylar cell disintegrates and the epidermal cells of the nucellus grow, there appears simply a small blue staining cavity between the embryo sac mother cell and the apical region of the epidermis, as cited by COULTER and CHAMBERLAIN (**15**) for *Clematis*, and *Helleborus* (GUIGNARD **20**), and *Delphinium* (MOTTIER **31**). The chalazal cell grows and its nucleus divides, completing the reduction division and giving rise to the 2-nucleate embryo sac (fig. 9). At this stage there is still something of the disintegrating micropylar cell to be seen, but at a slightly later stage it has entirely disappeared (fig. 10). The embryo sac is thus derived from two megaspores as in *Viscum articulatum* (Treub **43**) of the Archichlamydeae and in *Trillium* (Heatley **26**) and several other monocotyledons.

The two megaspore nuclei move to the opposite poles of the sac and divide (fig. 10). At this stage the sac is vacuolate and continues so until a late 4-nucleate stage (figs. 11–13). The 8-nucleate stage follows rapidly upon the four. Two-, 4-, and 8-nucleate stages have all been found in the same ovary, the 2-nucleate stage being at the base of the loculus. It is very easy, in serial sections, to confuse an early 8-nucleate stage with a late 4-nucleate stage, as the sacs have the same shape and cytoplasmic appearance.

In *Eriocaulon septangulare* (Smith **40**) the central vacuole first appears at the 4-nucleate stage. In *I. Sultani* the late 2-nucleate sac is vacuolate with large vacuoles between the two nuclei, but there is not one large central vacuole until the female gametophyte has been organized (figs. 10–14, 17). In an early 4-nucleate stage there are several large vacuoles extending along either side of the row of nuclei (fig. 11). During the 4-nucleate stage the sac enlarges, the cytoplasm becomes more dense, and the large vacuoles decrease (figs. 12, 13). By the time the 8 nuclei are formed the cytoplasm is very dense and contains a large amount of stored food, and the vacuoles have become small and inconspicuous (fig. 14). Very soon, however, a large central vacuole appears (fig. 17). The time of the inception of this central vacuole varies considerably. It may arise while the antipodal polar is at the base of the sac, or it may not appear until the polars are in contact and near the egg (figs. 14, 17, 18).

After the organization of the 8 nuclei the egg apparatus soon forms. The egg is more or less pear-shaped, with the larger end extending down below the synergids. The nucleus and greater part of the cytoplasm are in this region and the narrowed part extends up back of the synergids and is vacuolate. It evidently resembles the egg of *Aster novae-angliae* (CHAMBERLAIN **12**) and that of many other plants as to shape and relation of nucleus and cytoplasm (fig. 17).

The nuclei of the synergids do not always have the same position (figs. 15–17, 19). In the youngest sac of the series (fig. 15) there is a large vacuole at the base of either synergid, with the nucleus above and near the micropylar end. Fig. 16 illustrates a condition in which the synergid nuclei have moved down halfway, and in one cell there is a vacuole on either side of the nucleus, while in the other there is a large vacuole below it but only a small one above it. In fig. 17 one nucleus has moved entirely below the vacuole and is near the membrane at the end of the cell, whereas the other nucleus is still between two or more vacuoles. In a much older embryo sac (fig. 19) the synergids are longer, the nucleus of each is at its base, and a large vacuole appears above the nucleus. At all stages in the growth of the egg apparatus the synergids contain a fairly dense cytoplasm at the apex. It seems clear that the position of the synergid nucleus varies in relation to the age of the sac; that at first it is near the micropylar end of the synergid and above the vacuole; that later it passes the large vacuole and moves down to the opposite end of the cell. When the egg apparatus is mature the two nuclei are at the base of the cells, near the egg nucleus, and just below the large vacuoles (fig. 19).

According to the literature on the subject the position of the synergid nuclei in different plants may vary in relation to the large vacuole of the cell, but I have found no suggestion that the variation in a given species represents different stages in development. CHAMBERLAIN (**12**) gives the situation of the nuclei in *Aster novae-angliae* as varying in position from one end of the cell to the other but most frequently near the middle, the large vacuole being usually at the chalazal end of the synergid. GUIGNARD (**19**) says that in the Leguminosae the vacuole is usually at the base of the cell and the nucleus is central, but the vacuole may sometimes be above the nucleus. BARNES (**6**) in *Campanula americana*, GUIGNARD (**24**) in *Hibiscus Trionum*, and STRASBURGER (**42**) in *Wikstroemia indica von Buitenzorg* find the nucleus above the vacuole; while PACE (**36**) finds the synergid vacuoles of *Parnassia* in various positions.

The antipodals are surrounded by denser cytoplasm than is present above them, and they appear rarely as separate cells with delicate walls separating them (fig. 18), or, as is more commonly found, the mass of cytoplasm with the 3 nuclei is more or less cut off from the rest of the sac by a membrane but the cells are not separated. In either case they are but short-lived and disappear soon after the egg apparatus is formed. The embryo sac then persists for a long time with but 5 nuclei. Miss RAITT says that the antipodals in *I. pallida* cannot be distinguished with certainty and are evidently transitory. This ephemeral nature of the antipodals is common among many of the angiosperms. In *Striga lutea* (MICHELL **29**) the 3 antipodal cells begin to disintegrate before fertilization. In *Richardia africana* (MICHELL **30**) the disintegration is somewhat earlier, evidently more nearly like *I. Sultani*. In this species the antipodals were never found to increase in size or number and grow into the adjoining tissue, as has been described by CHAMBERLAIN (**12**) and OPPERMAN (**34**) for *Aster novae-angliae* and by others for various plants.

Very quickly after the 8 nuclei of the sac have been formed the antipodal polar moves up toward the micropylar polar and the 2 nuclei remain near each other at a short distance below the egg nucleus for some time. The nuclei may or may not be spherical, but they always contain a prominent nucleolus with a small highly refractive spot at the center. The chromatic substance of the polar nuclei is small in amount and forms either a delicate network lying just within the nuclear membrane, or a few strands radiating out from the nucleolus. Most of the food stored in the sac at an earlier period disappears before the female gametophyte reaches maturity and the sac becomes very vacuolate, with only a layer of cytoplasm at its periphery and surrounding the nuclei in the micropylar half of the sac (fig. 37).

During the later development of the embryo sac its shape becomes much changed (figs. 17, 19, 37). While the antipodals are still present the sac is a little over three times longer than wide, with the micropylar and antipodal ends both rounded in outline (fig. 17). After the antipodal cells disintegrate the basal region of the sac grows down into the chalaza. The growing portion is blunt or more or less triangular in outline, and but little narrower than the sac just above. The antipodal growth continues until the sac is over five times as long as it is wide (fig. 19). Following the development of this antipodal haustorium the sac widens in the region of the polar nuclei and assumes its mature shape (fig. 37).

During the origin and development of the female gametophyte the megasporangium has been undergoing marked changes. The ovule begins to curve before the megaspore mother cell appears, and by the time its nucleus has reached the segmented spirem stage the ovule has attained the anatropous position. At this time the inner integument extends beyond the nucellus and forms a fairly deep micropyle (figs. 1–4, 6). The outer integument arises from the lower two-thirds of the inner integument, appearing as a swelling from the outer part of the latter (fig. 6). This swelling increases greatly in breadth and grows up until its apex is on a line with the tip of the inner integument. It never grows beyond this point to aid in forming the micropyle, and the two integuments become distinct only at the summit (figs. 9, 37).

The origin of the outer integument in *I. Sultani* differs from the majority of plants and from the other species of *Impatiens* that have been studied. Miss RAITT (**37**) in *I. pallida* and GUIGNARD (**22**) in *I. parviflora* both show the outer integument arising from the basal portion of the ovule and remaining throughout its length distinct from the inner. As a result of his study of *I. balsamina*, BRANDZA (**9**) states that the Balsaminaceae have but one integument, but BRUNOTTE (**10**) disagrees with BRANDZA and gives two integuments for this family. According to LONGO,[1] as cited by Miss RAITT, this is the rule for the genus *Impatiens*, but the origin of the outer integument and its extension at the micropylar region appear to vary. From my study of the ovule of *I. Sultani* it can readily be seen how BRANDZA thought there was but one integument if *I. balsamina* is similar to *I. Sultani* in having the outer integument an outgrowth of the inner integument with only their tips free.

[1] LONGO, B., Richerche su le *Impatiens*. Annali Bot. **8**:65–77. 1909.

In *De l'ovule*, Warming (**45**) notes a few exceptions to the usual order of development of the integuments and gives *Viola*, *Ficus*, *Convallaria*, and *Orchis* as having two integuments which appear to grow as a single organ, and *Tropaeolum* as having at first two integuments which later appear as one. Warming quotes Strasburger as saying that in *Delphinium* the integuments originate as one and elevate themselves as a unit; later at the summit the two integuments become distinct. Judging from his figure the conditions in *Delphinium* are much the same as in *I. Sultani*.

As given earlier, the megaspore mother cell when it arises is completely surrounded, except at its base, by the epidermis of the nucellus, and the developing embryo sac also continues to lie in direct contact with the epidermis (figs. 2–4, 6, 8, 9). During the 2-nucleate stage of the embryo sac the epidermis begins to break down. The disintegration first appears as a flattening of the cells and nuclei just below the apex, and then extends gradually to the base of the embryo sac (figs. 9, 10, 14, 37). In *Oxalis corniculata*, according to Hammond (**25**), the epidermis, which in this case serves as a tapetum, begins to disintegrate before the 2-nucleate embryo sac is formed.

The apical cells of the epidermis are often longer-lived than those just below them, for it is quite common to find two or three cells surmounting the embryo sac and connected by only a line with those still persisting about the center of the sac (fig. 12). A somewhat similar appearance has been described by Smith (**40**) for *Eriocaulon septangulare*, where "the nucellar tissue lateral to the megaspores breaks down and is absorbed by the growing embryo sac. A few of the apical cells of the nucellus persist for a long time and enlarging assume the appearance of a tapetum. These too are ultimately absorbed and the embryo sac abuts directly upon the inner integument and micropyle." In *I. Sultani*, however, these apical epidermal cells do not enlarge and seem to have no special function.

While the epidermis continues to disappear it leaves but a line around the upper half of the sac (fig. 10). As the disintegration progresses downward, the cells near the base of the sac possess their normal tabular shape, while those nearer the middle of the sac are narrowed and pointed. The nuclear substance in the pointed cells is dense, the nuclei are often flattened, and the cell content stains but slightly. The pointed end of the layer often becomes free from the embryo sac (fig. 13). As this layer is disappearing it is not always in close contact with the tapetum (fig. 10), and I infer that the disappearance of the epidermis is due, not to its being crushed between the tapetum and the enlarging embryo sac, but rather to the fact that it is being absorbed by the embryo sac. The basal portion of the epidermis continues to exist until after the 8-nucleate sac is formed (fig. 14).

Not only is the entire epidermis absorbed eventually but the nucellus beneath the embryo sac also. During the early stages in the development of the embryo sac the cells of this part of the nucellus are similar to those of the interior of the integuments, but beginning with the 4-nucleate stage, or occasionally earlier, they become stringy in appearance, with their long diameters in line with that of the sac. This strand of cells extends down to the chalaza which is composed of a tissue of regular, compact, densely staining, isodiametric cells (figs. 12, 14, 37). Many of the nuclei of the "stringy" cells show signs of disintegration. They become dense, lose their rounded outline, and appear elongated. These cells are bounded at the sides by the tapetum (fig. 14). The antipodal region of the sac absorbs this tissue and pushes down to the nutritive cells of the chalaza, thus completing the absorption of the entire nucellus (fig. 37). *I. Sultani* agrees with *I. parviflora* (GUIGNARD **21**) and *I. amphorata* (LONGO **28**) in having the embryo sac absorb the nucellus and thus come in contact with the micropyle and the inner integument. These species of *Impatiens*, therefore, agree with the Compositae (GOLDFLUS **17**) in the early disappearance of the nucellus.

As described by GUIGNARD (**22**), RAITT (**37**), LONGO (**28**), and BRUNOTTE (**10**) for *Impatiens*, and by others for various angiosperms, the epidermis of the inner integument forms the tapetum of regular tabular cells, which, in *I. Sultani*, extend from the base of the micropyle to a considerable distance below the base of the developing embryo sac (figs. 9, 10, 14). The tapetum loses its uniform character as early as the 2-nucleate stage of the embryo sac, when a densely staining substance appears between the tapetal cells near the base of the micropyle and the contents of these cells stain diffusely. This appearance also extends out laterally and at this time up to the tip of the inner integument (fig. 9). The cells are crowded and their cytoplasm and nucleoplasm stain so diffusely that no attempt was made to represent their appearance in a sketch. As will be seen later, these cells break down during endosperm formation, and this doubtless represents an early stage in their disintegration. This characteristic progresses chalazally in the tapetal cells as the embryo sac develops and reaches the basal cells during early endosperm formation.

In an 8-nucleate stage the lower half of the tapetum is still normal and contains a decidedly granular cytoplasm and nucleoplasm which suggests the presence of food particles. This granular appearance is not visible in the cytoplasm of the other cells of the inner integument, although they stain more densely than do those of the outer integument. GUIGNARD (**22**) says that a nitrogenous substance accumulates in the tapetal cells of *I. parviflora* and that in all of the Balsaminaceae there is this proteid layer of tabular cells.

BILLINGS (**7**) believes with most students that the tapetal layer, whether from the inner integument or the nucellus, serves a nutritive function, dissolving and absorbing nutriment from the surrounding integument, and that its function is not simply protective, as given by HEGELMAIER (**27**). VANDENDRIES (**44**) in a study of the Cruciferae finds the tapetum a part of the inner integument, but believes it plays only a protective function. One reason given is that in the antipodal region, where the tapetum is separated from the sac by a small mass of nucellar cells, it presents the characteristic appearance of young and active tissue. This reasoning does not seem conclusive to me, since it may well be that this was a region of considerable food and that here the active cells of the tapetum digested and absorbed it and then passed it up to the embryo sac. In *I. Sultani* the tapetum persists longer at the antipodal end and it is here that growth takes place until the sac reaches the chalaza and passes slightly beyond the end of the tapetum.

BALICKA-IWANOWSKA (**5**) studied certain "Gamopetales" and described the tapetum. In agreement with CHODAT (**13**) and most recent writers, he does not believe that the tapetum is for protection, as it is wanting in the vicinity of the haustorium, which does not possess cell walls and would therefore appear in need of protection. He thinks that the tapetal cells possess a ferment in their mucilaginous content and exercise a digestive function, for they persist while the neighboring tissue disintegrates, and they surround the parts which are in the process of rapid growth.

Extending through the raphe is a strand of cells which is surrounded, except at the ends, by a layer of cells with cutinized walls. This strand terminates at the chalaza in the tissue of regular compact cells. It is into this that the antipodal region of the sac pushes (fig. 37). In looking at the figure it will be seen that the outer layer of cutinized cells ends just as it passes this area, and on the inner side the layer ends almost in contact with the antipodal end of the tapetum. It thus forms a protective covering to the conducting tissue as it passes to the chalazal haustorium. No true vessels were ever observed in this strand of conductive cells.

As noted earlier, the antipodal nuclei disappear before the haustorium develops, thereby giving rise to the unusual condition of a haustorium unaccompanied by nuclei. In none of the literature studied was I able to find any record of a similar condition. In the cases where a haustorium has developed at the antipodal region before fertilization had occurred, it is usual for the antipodal nuclei to be present in the haustorium formed. An interesting example of this is given by SOUÈGES (**41**) for the Solanaceae, where a pocket is formed at the basal part of the embryo sac and the antipodals take their place in the bottom of this and their digestive juices diffuse into the tissue beneath and dissolve out a cavity. The process of dissolution of the tissue varies among the different members of the family from a simple disjunction of the digestive layer of cells to a chalazal cavity whose capacity is comparable to that of the embryo sac itself, as in *Lycopersicum esculentum*.

Stamen

The flower possesses 5 stamens whose anthers are connivent and form a hood over the pistil. In a cross-section of a bud the sides of two adjacent anthers show as having their cells in contact, and this region appears as solid tissue. Each anther contains 4 microsporangia. Fig. 20 shows a cross-section of one-quarter of an anther when the nuclei of the microspore mother cells are in the synaptic state. The walls of the cells of the epidermis are cutinized and thicker than those of the other cells. The wall of the microsporangium consists of two distinct regions, the outer irregular portion made up of 1–5 layers of nearly isodiametric cells, and an inner region about 2 cells thick, the cells of which are flattened tangentially. This flattening, doubtless, results from the pressure caused by the growth of the archesporial and tapetal cells.

The microspore mother cells are separated from this inner wall by the tapetal cells. The latter, however, are not limited to the peripheral region, but extend into the mass of sporogenous cells and in some cases ramify entirely through the loculus, occupying more than one-half of the sporangial cavity. The origin of the tapetum was not definitely determined, but it seems highly probable that it arises from the sterilization of sporogenous tissue rather than from the inner cells of the wall, and that all of the sterile cells within the sporangium are of the same ancestry. The tapetal cells vary in size, many of them being as large as the microspore mother cells. They are binucleate and are more vacuolate than are the functional spore mother cells. The two nuclei of a single cell are usually side by side either at the center of the cell or at one end. Each nucleus contains one nucleolus or occasionally more.

CALDWELL (11) describes a condition for *Lemna minor* in some respects similar to that just outlined. He finds that during the early stages of the heterotypic division the cells of the tapetum sometimes divide and form groups of cells which project into the mother cell region; that the number of microspore mother cells is not reduced by the presence of the tapetal cells, although only a comparatively few developed spores, the others disorganizing and aiding the tapetum in nourishing the functional mother cells. In *I. Sultani* only about half the number of microspore mother cells arise that one would expect from the size of the sporangium. As indicated, not all of the tapetal cells arise at the periphery of the sporogenous mass, but many of them originate side by side with the microspore mother cells. The small number of microspore mother cells may doubtless be related to the probable hybrid nature of the form of *Impatiens Sultani* used. The distinction between the functional and non-functional sporogenous tissue can clearly be seen at an early stage, and still shows distinctly when the spore mother cells are in synapsis. The latter are still angular and are only just beginning to separate (fig. 20).

As is customary at the time of synapsis, the chromatic substance is massed against the nuclear membrane, with the single large vacuolate nucleolus projecting out from one side. As the prophase of the heterotypic division advances and a delicate spirem fills up the nuclear cavity, the cells become almost entirely free and round off, while the tapetal cells still remain somewhat angular in outline and often contain more than the 2 nuclei of the earlier stage (fig. 21). Their nuclei have become granular, lack a nucleolus, and stain more densely than before. In general, the entire mass of cells has separated from the wall. The ovule at this age shows no sign of the inner integument.

As the anther increases in size, the microspore mother cells become entirely rounded off and the spirem takes on a double appearance, whether due to a splitting of a single spirem or an approximation of two was not apparent. At this time the spirem is thicker and less delicate than the spirem immediately following synapsis (figs. 21, 22). The cytoplasm has an obscurely radiate appearance, being densely granular about the nuclear membrane and more vacuolate toward the cell membrane. The spirem thickens, becomes irregular, and segments transversely into bivalent chromosomes. The majority of the segments come to lie against the nuclear membrane and show clearly their double nature in the forms of X's, Y's, and V's. They are rough in outline and are connected here and there by delicate threads (fig. 23), similar to those figured by MOTTIER (33) for *Acer Negundo* and *Staphylea trifolia*. The nucleolus still persists and at this stage there may be two, a large and a small one.

The granular area surrounding the nucleus has become still more marked and closely resembles the kinoplasmic region described by ALLEN (1) for the pollen mother cells of *Larix* and by numerous other writers. The peripheral cytoplasm with its large meshes draws away from the cell membrane at various points. At this stage cellulose begins to be deposited about the cell and when the chromosomes have reached the equatorial plate a broad cell wall of cellulose is formed (fig. 27). As the chromosomes shorten and thicken, they become smooth in outline and numerous fibers heavier and longer than those mentioned for an earlier stage (fig. 23) appear within the nuclear cavity. These fibers seem to have no apparent relation to the fibers of the kinoplasmic region, although at this time the nuclear membrane has become indistinguishable from the cytoplasm at various places (figs. 24, 25). The fibers are tufted and may extend from a given chromosome across the nuclear cavity to other chromosomes or to the nuclear membrane. At this time no nucleoli are visible within the nuclei and there is the possibility that their substance has assisted in the formation of the fibers.

After the nuclear membrane has entirely disappeared many fibers appear about the chromosomes (fig. 26). They extend beyond what was the original area of the nucleus and doubtless there has been a union of intra- and extra-nuclear fibers in the formation of the multipolar spindle (fig. 26). By the time metaphase is reached the spindle has become sharply bipolar and extends across the entire cell (fig. 27). The cytoplasm surrounding the spindle has lost the dense granular appearance of the early prophase stages and stains less densely than does the peripheral region.

While I am not willing to make an unqualified statement regarding the number of bivalent chromosomes, it seems most probable from the study of the heterotypic divisions in the megaspore and microspore mother cells that the haploid number is 7, as I have been unable to count more than that number. No stages in microsporogenesis were obtained between metaphase of the heterotypic division and the tetrads following the homotypic division.

When the tetrads are formed the microspores are surrounded by the very thick cellulose wall of the mother cell. Each microspore is a little over 3 times longer than wide and possesses a reticulated membrane. At this time its nucleus is not spherical, but simulates the outline of the cell and its chromatic material is distributed unevenly throughout the nuclear cavity. Several large masses of chromatin are mingled with chromatic threads which extend out from them in various directions (figs. 28, 29).

The loculi containing these tetrads also contain densely staining tapetal cells. These cells still have large vacuoles, but the cytoplasm stains more densely than in earlier stages and their nuclei contain one nucleolus each. Outside the tapetum is the flattened layer of cells, and beyond this the remainder of the wall is still undifferentiated.

Later, when the microspores have broken away from the old mother wall, the endothecium with its spirally thickened cell walls forms just beyond the flattened layer. The tapetal cells, in general, are still in good condition, some of them centrally located having increased very greatly in size and number of nuclei. Compare the tapetal cell (fig. 33) which was magnified 810 times with the microspore (fig. 30) which was taken from a loculus ot the same age and magnified 1620 times. The number of nuclei in these tapetal cells may reach as high as 11 or more. These unusually large cells show stages in disintegration, and it is difficult to find one which has not begun to break down. A large number of nuclei, ranging from 6–13 in the tapetal cells of *Hepatica acutiloba*, has been reported by COULTER (**14**). SCHAFFNER (**39**) in his description of *Typha latifolia* states that the tapetal cells increase greatly in size while the tetrads are forming, but speaks of but 2 nuclei being formed in each cell.

When the microspores escape from the tetrad the chromatin of their nuclei consists of heavy, anastomosing strands which soon give rise to several distinct masses of chromatin connected with each other by more or less delicate threads. In by far the greater number of cases, if not always, these masses correspond in number with the haploid number of chromosomes (fig. 30). No nucleolus is visible at this time. There is evidently no true spirem formed in the division of the nucleus to form the generative and tube cells, but the rather imperfect reticulum of the very young microspores gives rise directly to the chromosomes at a considerable time before the organization of the spindle. It is a very common occurrence to find all the microspores of an anther in an apparently resting stage and showing distinctly 7 chromatic masses.

The microspore divides and forms a more or less vacuolate 2-celled pollen grain (figs. 31, 32). The tube nucleus is normally spherical and lies more or less near the center of the developing pollen grain (figs. 32, 34, 35). The generative cell occupies various positions within the cytoplasm of the tube cell, and at all times its nucleus is smaller and its reticulum is much less delicate than that of the tube nucleus. The pollen grain grows and its cytoplasm becomes densely filled with food granules. At this time the generative cell may either be attached to the wall of the pollen grain or lie free in the cytoplasm (figs. 34, 35).

When the anther is ready to dehisce, it is impossible to distinguish the cytoplasm of the generative cell, and its nucleus has changed from nearly spherical to a very slender lunate form (fig. 36). At first it was thought to be a sperm nucleus, but while these crescent-shaped nuclei are very characteristic of the developing male gametophyte, no more than one to each pollen grain was ever found. When the nucleus is in this condition it contains several chromatic masses in the center and stains a diffuse yellow at either end. In all cases where the nucleus could be seen clearly throughout its entire length 7 chromatic masses were visible (fig. 36). The mature pollen grains, in longitudinal section, present an almost rectangular appearance and possess 4 germ pores, one at each corner. No instances of the division of the generative cell while still within the anther were discovered, and it is doubtful whether this division takes place until some time after pollination.

Ovule after pollination

The pollen tube enters the embryo sac after the chalazal haustorium has developed. Many of the embryo sacs of a given ovary were found containing the pollen tube contents in their micropylar region. While no experiments were made to eliminate all chance of cross-pollination, the conditions under which these plants were grown in the greenhouse render it very probable that many of the flowers were self-pollinated. The pollen tube enters the embryo sac at one side of the filiform apparatus and either continues down the same side of the sac near to the region of the egg nucleus or crosses over the synergid and extends down the other side (figs. 37, 38). After this has occurred it is difficult to find both of the synergid nuclei. Doubtless one of them soon becomes disorganized, due to the effect of the presence of the pollen tube. SMITH (**40**) describes the pollen tube of *Eriocaulon* as either passing through a synergid or between the two without destroying them.

In *I. Sultani* the tube nucleus was usually visible in the embryo sac, but it was often difficult to discover the sperms, due to their small size and also to the presence of many small densely staining bodies which often suggested parts of nuclei but were possibly food particles. The sperms are coiled or spiral in outline as they approach the egg and polar nuclei. In fig. 38 the two sperms are both near the egg nucleus, one is directly over the latter and the other is at its side, still in the dense strand of cytoplasm which marks the path of the pollen tube contents, and doubtless is on its way to the two polar nuclei. No sperm cytoplasm is visible and the nucleus is a spiral body made up of dark and light areas, the former of which are doubtless masses of chromatin. The character of the sperm shown in fig. 39 differs somewhat from those in the preceding figure. Here a sperm nucleus is situated one at either side of the egg nucleus; the one at the right is coiled tightly and shows no distinction between chromatic and clear areas, but stains a clear light blue. It was doubtless on its way through the cytoplasm at the side of the egg to the endosperm nucleus lying directly below the egg.

No stages in the actual fusion of the egg and sperm were seen. The fertilized egg differs so slightly from the unfertilized one that it is difficult to decide in a given case whether or not fertilization has occurred. In general, however, the fertilized egg increases slightly in size and its limiting membrane is more conspicuous than it is in earlier stages (fig. 40). Figs. 38 and 40 have the same magnification and the increase in size is evident.

It seems probable that the polar nuclei unite at an early stage in the fusion of the sexual nuclei. The nuclear membranes of the two polars break down where they come in contact and one of the nucleoli passes over into the other nucleus (figs. 41, 42). Both nucleoli possess one or more vacuoles. What appears to be a later stage in the fusion of the two polars is given in fig. 43. A dense granular mass, the entering nucleolus, seems to be in vital contact with the nucleolus of the receiving nucleus and gives the impression of giving of its substance to help in the formation of the nucleolus of the resulting endosperm nucleus. The characteristically large vacuole of the primary endosperm nucleolus has already appeared. Not all of the entering nucleolus fuses with the receiving nucleolus, however, for coarse strands radiate out from the dense mass of nucleolar substance and appear to be adding to the reticulum of the nucleoplasm. A similar radiating mass has been observed in one of two polars. In this case it might represent a stage in the fusion of the second sperm with one of the polars before the two polar nuclei had united. Similar masses have also been seen in the megaspore mother cell, and here also the nucleolus doubtless contributes to the chromatic substance.

The fusion of the two polars has been figured by numerous writers for many different plants. In *Nicotiana Tabacum* (GUIGNARD **23**) the two nucleoli remain distinct in the fusion nucleus for some time before fusing. VANDENDRIES (**44**) figures for *Cardamine pratensis* two nucleoli within the primary endosperm nucleus with a sperm against one side of it. He says that when the pollen tube enters the cavity of the embryo sac the two polar nuclei have begun to fuse but the nucleoli are still distinct. In *I. Sultani*, however, the fusion of the two polar nuclei begins relatively much later and takes place very quickly. In describing the fusion of the two polars of *Arisaema triphyllum*, GOW (**18**) says that the fusion endosperm nucleus frequently contains two nucleoli.

It seems highly probable that after the primary endosperm nucleus is formed the second sperm unites with it. By this time the sperm nucleus appears to be larger than it was in earlier stages. In fig. 44 it is just at the point of piercing the nuclear membrane, and in fig. 45 it is within the primary endosperm nucleus and lying either above its nucleolus or within it. It was impossible to determine if the second sperm, in all cases, waited until the primary endosperm nucleus was formed before becoming functional. GUIGNARD (**23**) is convinced that in the Malvaceae the time of formation of the secondary nucleus is constant for a given genus. In *Lavatera* and others it is formed before fertilization, while it is formed after in *Hibiscus*.

Following fertilization a micropylar haustorium is formed. The primary endosperm nucleus divides before the division of the fertilized egg. After a few divisions have taken place several of the resulting endosperm nuclei pass up through the micropylar part of the embryo sac (figs. 46, 47) out into the micropyle and form a haustorium which emerges from the micropyle and crosses over the space between the latter and the funiculus (figs. 49*a*, *b*). As the haustorium encounters the funiculus it either extends along the funiculus some little distance before entering it or penetrates it immediately and branches freely within its tissue (fig. 53).

In the early stages, as the endosperm nuclei pass through the upper part of the sac, they are surrounded by cytoplasm rendered dense by the presence of a large amount of food substance and consequently the nuclear membrane is entirely obscured (figs. 46, 47). The densely staining filiform apparatus, all that remains of the two synergids, is still present, but it is more widely separated from the enlarged part of the embryo sac than in earlier stages (fig. 47). The narrow micropylar part of the sac where the synergids of the mature embryo sac were situated has widened and encroached upon the small disorganizing cells of the inner integument. These cells have now disappeared except for a few remains and large regular cells limit the micropylar cavity into which the sac has pushed (cf. figs. 9, 14, 47). At this stage the fertilized egg is still undivided and several endosperm nuclei lie below as well as above it. These nuclei are not shown in fig. 47, as they occurred in a different section from the one sketched.

In the later stages in the development of the micropylar haustorium but few nuclei are present in it. These are very large and contain a large nucleolus and stain bright red with safranin (fig. 53). This haustorium was seen to persist up through the oldest stages studied, namely, those containing embryos with radicle and cotyledons differentiated.

The micropylar haustorium of *I. Sultani* differs from that of *I. amphorata*, as described by LONGO (**28**), in not entering the outer integument. It simply pierces the funiculus and branches extensively within it.

As in *I. amphorata* (LONGO **28**), *I. Sultani* possesses a chalazal haustorium as well as a micropylar one. This haustorium is much less extensive than is the micropylar one. One of the endosperm nuclei at the antipodal region becomes very large, and with its surrounding cytoplasm forms a long cell which pierces through the sac and one end of it enters the chalazal tissue, while the other end remains in contact with numerous normal endosperm cells (figs. 50, 51, 53).

It was difficult to secure a vertical section through this haustorium, as a series of sections which cut through the embryo vertically would section the haustorium somewhat diagonally. Fig. 50 shows the outline of the cell, but no nucleus, while fig. 51 shows the embryo sac portion with a large nucleus, but the chalazal part was cut so that all connection between chalazal tissue and haustorium was lost. This large haustorial cell contains a densely granular cytoplasm and is doubtless active in conveying nutriment from the chalaza to the endosperm. This haustorium does not remain active as long as the micropylar one. By the time the cotyledons of the embryo have become differentiated it is not so prominent as in earlier stages, while the micropylar haustorium still seems very active (fig. 53).

The endosperm develops more rapidly at the micropylar and chalazal regions than at the sides of the sac. A layer of cytoplasm with a single row of free nuclei persists at the sides for some time, while at the poles of the sac walls come in early to separate the nuclei (figs. 49*a*, 50, 51). With the presence of two rows of nuclei at the sides, walls form about the outer layer of nuclei, while those of the inner layer remain free (fig. 48) until some time later, when they are separated by walls, and the endosperm is composed entirely of cells (fig. 53). The size and shape of the embryo sac have undergone marked changes during endosperm formation. At the time of fertilization the outline of the sac is similar to that shown in fig. 54, with the early antipodal haustorium opposite the micropylar part of the sac. Later, during early endosperm formation, the sac elongates and widens slightly at the micropylar region. Below this it enlarges considerably on the side away from the raphe, and the sac becomes asymmetrical (fig. 55). This lateral growth continues until it extends even beyond the original position of the antipodal haustorium, with the result that the chalazal haustorium of endosperm origin comes to lie at the side of the sac rather than at its base, and the embryo sac extends below the chalaza (fig. 53).

The embryo develops less quickly than does the endosperm. As stated earlier, the fertilized egg does not divide until after many free endosperm nuclei have been formed. The proembryo becomes differentiated into suspensor and embryo early in its development. By the time the embryo consists of several cells the suspensor, in a longitudinal section, shows but two cells. The cell adjoining the embryo is broader than long and the terminal one is but slightly longer than wide (fig. 49*a*). The suspensor, doubtless on account of the very effective micropylar haustorium, appears to be but a short-lived organ. It neither elongates nor becomes bladder-like, as is the case for many of the angiosperms, but soon breaks down and disappears. It shows signs of disintegration before the cotyledons of the embryo appear (fig. 52), and by the time they are differentiated the suspensor has disappeared. The embryo develops at the tip of the suspensor and by the time the endosperm consists of two layers of cells about the periphery of the embryo sac the radicle and two cotyledons have become differentiated (figs. 53, 56).

The embryo and the chalazal haustorium do not occur in the same vertical plane, therefore it is impossible to secure satisfactory sections of the two from the same embryo sac. In the oldest stage studied a band of endosperm cells lines the sac (figs. 53, 56). The endosperm lies in close contact with the axis of the embryo and the sides of the cotyledons, but it is separated from the chalazal end of the embryo by a large cavity. Unfortunately, through lack of study of the seeds of *I. Sultani*, I was unable to determine the fate of the endosperm. According to GUIGNARD (**22**), a thin layer of endosperm remains undigested in the mature seed. BRUNOTTE (**10**), from his study of the Balsaminaceae, believes that the descriptions of the systematists for the mature seed should be changed.

Instead of describing the seed as having no endosperm, he would say that there is a small amount of endosperm present.

Summary

1. The ovule possesses but one hypodermal archesporial cell.

2. The archesporial cell is also the megaspore mother cell.

3. An axial row of two cells is formed. The chalazal cell is the mother of the embryo sac.

4. A normal 8-nucleate sac is formed.

5. There is a variation in the position of the synergid nuclei, due to their age.

6. The two polar nuclei come in contact directly beneath the egg and do not fuse until after the pollen tube has entered the embryo sac.

7. The 3 antipodals may be either 3 cells or a group of 3 nuclei cut off from the upper region of the sac by a membrane.

8. The antipodals disappear soon after the egg apparatus is formed.

9. The megaspore mother cell and the early 2-nucleate embryo sac are bounded at the apex and sides by the nucellar epidermis.

10. The embryo sac absorbs the nucellar epidermis and by means of an antipodal haustorium absorbs all of the nucellus between the sac and the chalaza.

11. The tapetum is derived from the inner layer of the inner integument.

12. The outer integument arises from the inner integument.

13. Binucleate tapetal cells surround the microspore mother cells. They also extend into the mass of sporogenous cells and separate the functional mother cells into groups.

14. The nucleus of the generative cell of the pollen grain apparently does not divide before pollination.

15. The pollen tube enters the embryo sac along the side of the filiform apparatus and extends down one side of the embryo sac until it is near the egg nucleus.

16. Two coiled sperm nuclei are often seen near the egg nucleus.

17. It seems very probable that triple fusion occurs.

18. An extensive micropylar haustorium and a more simple chalazal one develop from the endosperm.

19. The embryo possesses a short suspensor.

20. The bivalent chromosomes in both megasporogenesis and microsporogenesis show X's, Y's, and V's.

21. A multipolar spindle appears in the prophase of the heterotypic division in microsporogenesis.

22. The nucleus of the microspore has but a short period of rest; the prophase of division is initiated early and persists for some time.

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EXPLANATION OF PLATES XIV, XV

All figures were drawn with the aid of an Abbé camera lucida and are reduced one-half in reproduction. The number accompanying the description of each figure indicates the magnification before the reduction. The lettering of the figures is as follows: *ii*, inner integument; *oi*, outer integument; *mc*, megaspore mother cell; *n*, nucleolus; *f*, funiculus; *ma*, micropylar cell of axial row; *e*, epidermis of nucellus; *t*, tapetum; *s*, stringy cells of the nucellus; *en*, egg nucleus; *sn*, synergid nucleus; *cv*, central vacuole; *p*, polar nucleus; *mm*, microspore mother cell; *dn*, disintegrating nuclei; *tn*, tube nucleus; *gn*, generative nucleus; s^1, sperm nucleus; s^2, sperm nucleus; *fa*, filiform apparatus; *ptc*, pollen tube contents; *rp*, receiving polar; *m*, micropyle; *ah*, antipodal haustorium; *mh*, micropylar haustorium; *ch*, chalazal haustorium; *sp*, suspensor; *c*, chalaza; *ed*, endosperm; *vs*, vascular strand; *r*, radicle; *co*, cotyledon; *w*, wall; *pe*, primary endosperm nucleus; *ra*, raphe; *cu*, cells with cutinized walls; *nrp*, nucleolus of receiving polar; *edn*, endosperm nuclei.

PLATE XIV

Fig. 1.—Vertical section of ovule before integuments have appeared; ×828.

Fig. 2.—Vertical section of ovule showing origin of inner integument and large megaspore mother cell; ×810.

Fig. 3.—Vertical section of ovule slightly older than fig. 2; ×810.

Fig. 4.—Vertical section of ovule with nucleus of megaspore mother cell in synapsis; ×810.

Fig. 5.—Vertical section of megaspore mother cell with nucleus in second contraction stage of prophase of heterotypic division; ×1620.

Fig. 6.—Vertical section of ovule showing origin of outer integument and segmented spirem of megaspore mother cell; ×500.

Fig. 7.—Vertical section of megaspore mother cell showing tetrad formation in nucleus; ×1300.

Fig. 8.—Vertical section of nucellus after 2-celled axial row has been formed; ×1300.

Fig. 9.—Vertical section of portion of ovule containing 2-nucleate embryo sac; ×1000.

Fig. 10.—Vertical section of 2-nucleate embryo sac with surrounding nucellus and tapetum; nuclei of embryo sac in prophase of division; ×810.

Fig. 11.—Vertical section of young 4-nucleate embryo sac; combination of 3 serial sections; ×810.

Fig. 12.—Vertical section of slightly older sac with nucellus and disintegrating epidermis; ×810.

Fig. 13.—Vertical section of still older 4-nucleate embryo sac with basal portion of epidermis still intact; ×1000.

Fig. 14.—Vertical section of early 8-nucleate embryo sac with nucellus at base and tapetum at either side; ×1000.

Fig. 15.—Vertical section of early stage in formation of egg apparatus: synergid nuclei each above a large vacuole; ×1000.

Fig. 16.—Vertical section of micropylar region of embryo sac showing 2 synergids; synergid nuclei have reached center of the 2 synergid cells; ×1000.

Fig. 17.—Vertical section of 8-nucleate embryo sac before the 2 polar nuclei have reached their position directly beneath egg; combination of 2 serial sections; ×1000.

Fig. 18.—Vertical section of antipodal region of 8-nucleate sac before antipodal polar has moved toward micropylar polar; the 3 antipodals show as distinct cells; combination of 2 serial sections; ×1620.

Fig. 19.—Vertical section of embryo sac after antipodals have disappeared and antipodal haustorium has begun to develop; micropylar tip of sac was covered by inner integument; ×1000.

Fig. 20.—Cross-section of microsporangium while spore mother cells are in synaptic stage; ×500.

FIG. 21.—Cross-section of contents of microsporangium soon after chromatic substance of microspore mother cells has formed a spirem following synapsis; ×500.

FIG. 22.—Section of microspore mother cell slightly older than those in preceding figure; nucleus contains spirem showing its double nature; ×1620.

FIG. 23.—Section of microspore mother cell soon after spirem has segmented; 2 nucleoli present, small one directly over large one was omitted from sketch; ×1620.

FIGS. 24, 25.—Sections of 2 microspore mother cells after bivalent chromosomes have shortened and become smooth in outline and intranuclear fibers have appeared; in fig. 25 a thick wall is beginning to form about the mother cell; ×1620.

FIG. 26.—Section of microspore mother cell with multipolar polyarch spindle; heterotypic division; ×1750.

FIG. 27.—Section of microspore mother cell showing bipolar spindle of heterotypic division; bivalent chromosomes arranged at equatorial plate; ×1620.

FIG. 28.—Cross-section of tetrad; ×1620.

FIG. 29.—Vertical section of tetrad with but 2 of the microspores visible; ×1620.

FIG. 30.—Vertical section of young microspore; nucleus has passed through a very short resting stage and has entered upon a prolonged prophase; ×1620.

FIG. 31.—Cross-section of young pollen grain; large central vacuole present and tube and generative nuclei at one side of pollen grain; ×1620.

FIG. 32.—Vertical section of slightly older pollen grain than fig. 31; generative cell lies near center of pollen grain; ×1620.

PLATE XV

FIG. 33.—Section of one of large multinucleate tapetal cells which occur within microsporangium after microspores have separated from tetrads; nuclei in various stages of disintegration; ×810.

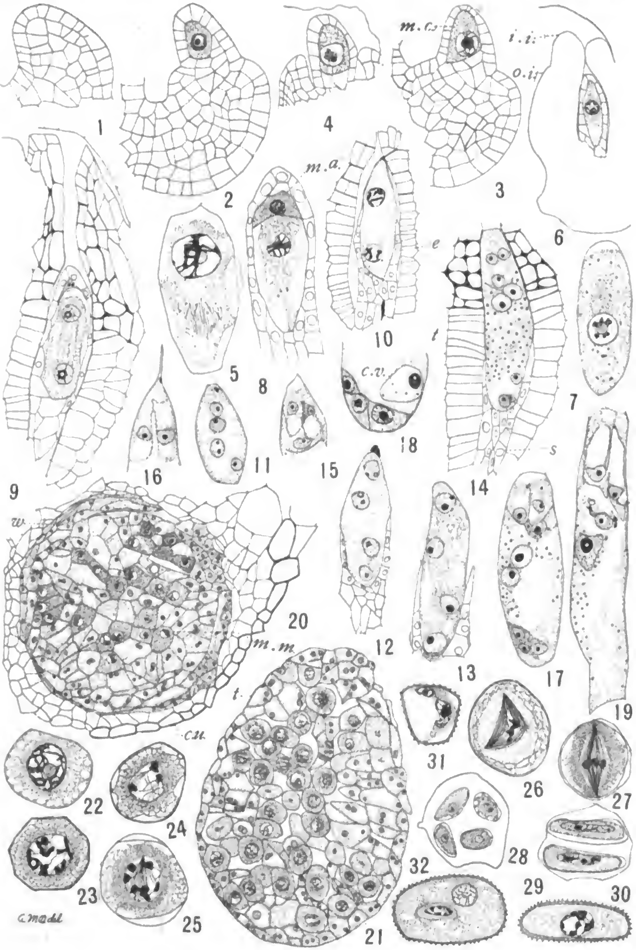
FIGS. 34, 35.—Vertical sections of nearly mature pollen grains; note change in size and cytoplasmic contents from fig. 32; cytoplasm packed full with food which is doubtless starch grains; in fig. 34 generative cell lies against wall of pollen grain, while in fig. 35 it lies free within cytoplasm of tube cell; ×1620.

FIG. 36.—Cross-section of mature pollen grain; cytoplasm of generative cell cannot be distinguished from that of tube cell; generative nucleus forms a crescent and contains 7 distinct chromatic masses; ×1375.

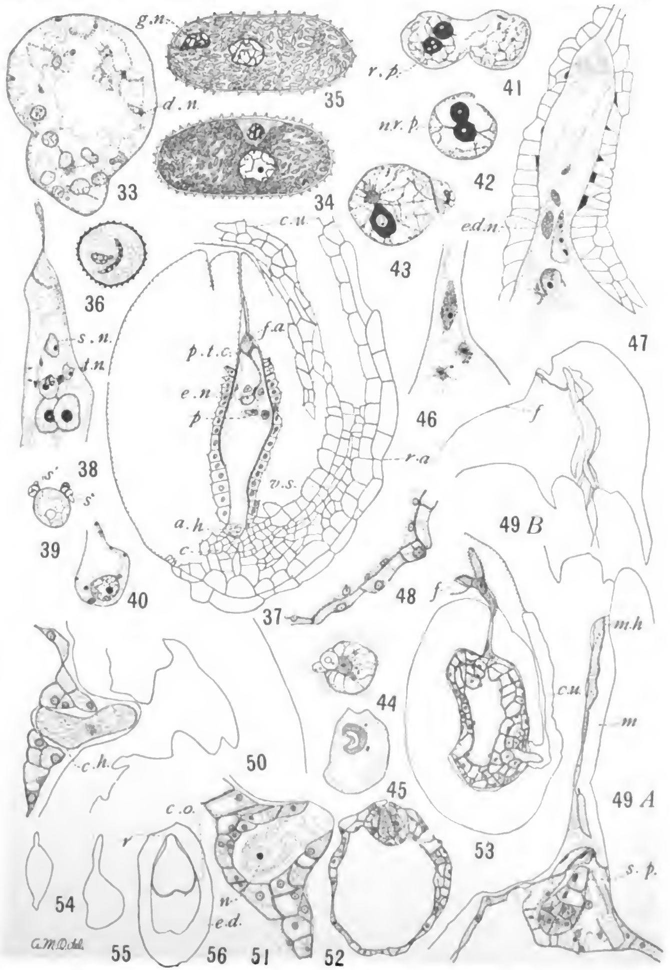
FIG. 37.—Vertical section of ovule after pollen tube has entered embryo sac; sketch is largely in outline and was derived from 3 serial sections; ×500.

FIG. 38.—Vertical section of micropylar region of embryo sac after pollen tube has entered sac; ×1000.

FIG. 39.—Two sperms near egg nucleus; ×1620.



OTTLEY on IMPATIENS



OTTLEY on IMPATIENS

FIG. 40.—Fertilized egg; ×1000.

FIGS. 41–43.—Stages in fusion of the 2 polar nuclei; ×1620.

FIGS. 44, 45.—Stages in fusion of second sperm nucleus with endosperm nucleus; fig. 44, ×1620; fig. 45, ×1625.

FIG. 46.—Vertical section of apex of embryo sac showing 3 endosperm nuclei on their way to form micropylar haustorium; another section shows endosperm nucleus below original position of primary endosperm nucleus; ×500.

FIG. 47.—Vertical section of micropylar portion of embryo sac after primary endosperm nucleus has divided several times; sac has enlarged beneath filiform apparatus; ×1000.

FIG. 48.—Portion of endosperm present at one side of embryo sac after embryo has formed; ×500.

FIG. 49*a*, *b*.—*a*, vertical section through micropyle with micropylar haustorium, and through embryo sac at base of micropyle; young embryo with short suspensor surrounded by endosperm cells; ×500; *b*, vertical section of micropylar haustorium as it extends across space from micropyle to funiculus; *a* and *b* are sketches of same haustorium, but taken from different sections; ×500.

FIG. 50.—Section through chalazal portion of ovule; chalazal haustorium and endosperm cells are filled in while only outline of chalazal tissue is given; sketch is from same ovule as fig. 49*a*, and is a combination of 2 sections; ×500.

FIG. 51.—Vertical section of chalazal haustorium with surrounding endosperm cells; haustorium cut somewhat diagonally; ×500.

FIG. 52.—Vertical section through embryo sac after a many-celled embryo has developed; endosperm at base and at one side consists of but one layer of cells, at the other side consists of several layers, and in another section of this same embryo sac chalazal haustorium occurs in this thickened portion of endosperm; ×162.

FIG. 53.—Outline sketch of vertical section of ovule containing embryo of 2 cotyledons; embryo does not show in section; combination of 2 sections; ×162.

FIG. 54.—Outline sketch of vertical section of embryo sac at time of fertilization or slightly later; growth has taken place at antipodal and at median regions; ×162.

FIG. 55.—Outline sketch of vertical section of embryo sac after embryo has been developed; narrow micropylar portion of sac has lengthened and increased somewhat in width; side opposite raphe has pushed out into integument, giving an asymmetrical sac; ×162.

FIG. 56.—Outline sketch of vertical section of embryo and accompanying endosperm tissue; embryo is differentiated into radicle, hypocotyl, and 2 cotyledons; ×162.

NOTES ON AMERICAN WILLOWS

II. THE SPECIES RELATED TO *SALIX GLAUCA* L.

CAMILLO SCHNEIDER

In my first paper[1] I dealt with *Salix arctica* Pall. and its relatives. These species are mostly united with *S. glauca* L. and its congeners in one group or section by such American salicologists as P. A. RYDBERG and C. R. BALL. European students of willows like N. J. ANDERSSON, A. and E.-G. CAMUS, and O. v. SEEMEN referred the two species to different sections, and I have always thought it best to regard each species as a representative of a distinct group. It is not an easy task to draw a line between the forms of the GLAUCAE on the one hand and those of the *arctica* group on the other, but this is true of most of the sections in a genus like *Salix*, where it is difficult to define groups of closely related species. As I have already explained in SARGENT, Pl. Wils. **3**:136. 1916, the name ARCTICAE is not available to designate the group of which *S. arctica* Pall. is the type, because it was first used by ANDERSSON (1858) for a section containing *S. Hookeriana* Barr., *S. speciosa* Hook. and Arn., non Host. (*S. alaxensis* Cov.), etc., which in 1868 ANDERSSON included in his sect. NIVEAE B. VILLOSAE; therefore I (*l.c.* 140) proposed the name DIPLODICTYAE for this group, but at this time I also kept the OVALIFOLIAE of RYDBERG as a separate unit, expressing, however, a doubt "whether the species united by RYDBERG in this section really belong in the same group." At present I believe that *S. ovalifolia* should be placed in the same section with *S. arctica*, and consequently the name OVALIFOLIAE must be adopted for this group. To distinguish between those two sections the color and pubescence of the bracts (or scales) seems to afford a rather reliable character. In the OVALIFOLIAE the bracts are usually more or less bicolor, being pale at base and dark brown, fuscous, or even blackish toward the apex, while the forms of the GLAUCAE mostly have uniformly yellowish, light brown, or straw-colored bracts, which sometimes (especially in the upper part of the ament) are reddish or purplish toward the apex, but never become really fuscous or blackish. Furthermore, the pubescence of the 2 kinds of bracts is of a different character. In the first group it usually consists of rather long, straight, silky hairs, of which at least the uppermost are about the same length as the bract, which mostly does not bear many short hairs on its surface, and often becomes nearly glabrous. In the second group the hairs are comparatively shorter, less straight, and rarely distinctly silky, but are softer and sometimes a little curly. As a whole the bracts are more or less covered with pubescence, and are rarely distinctly ciliated at apex with long silky hairs. These characters are usually more easily detected in the female than in the male specimens, which are often more similar in the two groups. It takes some time for the student to become familiar with these peculiarities, which are by no means clearly recognizable in every specimen. There are of course exceptions also, but in such cases we find other characters to determine the real affinity of a certain form. Many so-called intermediate forms are of hybrid origin, or should receive closer observation in the field before defining their taxonomic position. This is what I have to say at present regarding the separation of the sections GLAUCAE and OVALIFOLIAE. Later I hope to have the opportunity to discuss in detail the systematic arrangement of the American species of *Salix*.

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[1] BOT. GAZ. 117–142. 1918.

As I now understand them, the following species belong to the section GLAUCAE: *S. anamesa* Schn., *S. brachycarpa* Nutt., *S. chlorolepis* Fern., *S. cordifolia* Pursh, *S. desertorum* Rich., *S. fullertonensis* Schn., *S. glauca* L., *S. lingulata* And., *S. niphoclada* Rydbg., and *S. pseudolapponum* v. Seem. I do not include in this group *S. chlorophylla* And., *S. McCalliana* Row., *S. Nelsonii* Ball, *S. saskatchavana* v. Seem., and *S. idahoensis* (Ball) Rydbg., which RYDBERG places in his section ARCTICAE (Fl. Rocky Mts. 190. 1917), which seems to me an unnatural mixture of species of different affinities.

1. S. GLAUCA L., Sp. Pl. **2**:1019. 1753.—Before we can decide whether any American forms or which of them are to be referred to this species it seems necessary to discuss the characters of the typical *S. glauca* L. It is founded on "363. *Salix* foliis integris subtus tenuissime villosis ovatis. Tab. VIII. fig. p. and Tab. VII.

fig. 5" in LINNAEUS' Fl. Lapp. 290. 1737. The description and figure given by the author in this place give a rather good idea of his type. Furthermore, ENANDER (Stud. Salic. Linnés Herb. pp. 51, 54, 59. 1917) describes the female and male specimens of *S. glauca* genuina, typica or vera in Linnaeus' herbarium. Following LINNAEUS and ENANDER, I find the following characters of what has to be called the typical *S. glauca:* Frutex bi- vel tripedalis. Rami rubescentes, glabri; ramuli novelli villosi. Folia ovata, lanceolata, ovali-lanceolata vel ovato-oblonga, utrinque fere aequaliter attenuata vel inferiora apice obtusa, superiora magis oblonga acutiora, integerrima, 15:8 vel 40:12 ad 60:15 vel 55:20 mm. magna, utrinque (subtus tamen densius) villosi vel superne pilis parcius obsita vel fere glabra, non vero nitida, subtus pallidiora, "villis oblongis raris hirsuta" vel "pilis albicantibus vestita"; petioli 8-10 mm. longi, villosi; amenta pedunculis ad 3 cm. longis foliolis circ. 4 ceteris similibus instructis suffulta; flores masculi bracteis pallidis pilosis, filamentis basi pilis crispatis ornatis antheris testacei coloris instructis; feminei bracteis similibus, ovariis capsulisve tomentosis sessilibus, stigmatibus stylisque quasi semipalmato-alcicornibus.

Not having sufficient herbarium material from Lapland at my disposal, I think it best to add the following characters given by ANDERSSON in his Salic. Lap. 73, *fig. 21.* 1845:

> Amenta serotina ramulos breves crassiusculos tomentosos foliis ceteris vix minoribus 3-6 vestitos terminantia, iisque plerumque longiora, cylindrica, obtusa, erecta, demum sublaxa; mascula 1-2 uncialia, densa, squamis oblongis, obtusis, fulvis apice roseis, pilis albis longis rectis villosissimis, stam. 2, filamentis fulvis, basi barbatis, antheris globosis prius coerulescenti-roseis; feminea subdensiflora, abrupta, obtusa, 1-3 uncialia, primum rigida, demum laxa, squamis fulvis apice roseis, oblongis, obtusis, ventrem capsulae superantibus, albo-villosis; capsulae pedicello nectario lato quadrangulari pl.m. profunde partito, dimidio breviori, brevissime pedicellatae, ovales vel conicae, obtusae, lana alba densissime tomentosae, stylis aut omnino geminis aut fere usque ad basin bipartitis (ut eorum pars, quando adest, semper sub lana capsulae lateat), stigmatibusque linearibus divaricato-bipartitis, rufo-fulvis terminatae.

Judging by these characters we have to decide, I believe, whether there are in America forms identical or closely related to the typical

S. glauca from Northern Europe. According to the leading European salicologists *S. glauca* is rather variable, but I fail to find a good arrangement of the different variations already known from Europe and Northern Asia in the existing literature. It is impossible to judge the American forms correctly without having a clear understanding of the Asiatic forms already described, because it is to be expected that the forms from Eastern Asia will have the closest affinity with the American forms.

No mention is made of *S. glauca* by PURSH (1814) or MICHAUX (1820), or even by HOOKER (1839). It was ANDERSSON who in 1858 first mentioned *S. glauca* as occurring "in provinciis septentrionalibus et arcticis Americae borealis." He further said:

> Haec species . . . . in arcticis regionibus Americae habitu externo vix nostrae similis exstat. Specimina tamen a Seemann in parte occidentali et a Lyall in Disco Island lecta, nec non e "Rocky Mountains" reportata cum nostris tamen ita congruunt, ut de identitate non dubitare liceat. Folia nunc utrinque molliter villosa et incana, nunc denudata subviridia, amenta semper foliato-pedunculata, capsulae brevius pedicellatae. Huic certissime ut forma tantum associanda—*villosa*. *S. villosa* (D. Don) Hook. *l.c.* p. 144, no. 3.

This *S. villosa* Barratt apud HOOKER has to be ascertained before anything else can be done to determine which forms may be referable to *S. glauca*. HOOKER (Fl. Bor.-Am. **2**:145. 1839) said: "that Dr. BARRATT considers it to be the same as *S. villosa* of D. Don, in Pursh, Herb. Canad." I have never seen specimens from a "Herb. Canad." of PURSH, nor do I know whether PURSH ever distributed such a collection.[2] Neither he nor D. DON published a *S. villosa;* there are, however, two species bearing this name, one of SCHLEICHER (Cat. Pl. Helv. ed. 3. 26. 1815) which is a nomen nudum and was probably first mentioned in the first edition of the Catalogue in 1809; the other of FORBES (Salict. Wob. 183. *pl. 92.* 1829) representing a sterile specimen of unknown origin. Thus the name *S. villosa* Barr. cannot be used even if the form described by HOOKER under this name could be recognized as a good species. I have been fortunate in seeing photographs and fragments of the types of *S. villosa* preserved at Kew, and also the corresponding specimens of BARRATT's collection in herb. N., and I am convinced that HOOKER included different forms under his *S. villosa*. At first glance his diagnosis fits well the forms described by RYDBERG as *S. Seemannii* (see later) and the material before me from the Yukon Territory, but the character given by HOOKER in the following phrase: "rami foliisque junioribus lana arachnoidea villosis" seems peculiar to me. I cannot detect traces of a "lana arachnoidea" on the specimens before me, and furthermore, the specimen collected by DRUMMOND (no. 7. Herb. H. and B.) which is regarded as the "type" is not characterized by "foliis lato-lanceolatis." There is, however, a specimen in Herb. Torrey (N.) labeled "no. 6. Herb. H.B. and T." and "an *S. villosa* D. Don" in which the lower surfaces of the lanceolate leaves are covered when young with a "lana arachnoidea," the prominent rib being nearly glabrous, while the lateral nerves are almost hidden by the pubescence. Later the leaves become more or less glabrous, and the first or lowermost leaves show nothing but a few scattered long silky hairs. The petioles are nearly glabrous, and the stipules are very small, hardly a fourth of the length of the petiole, very glabrescent, semiovate, and denticulate. This does not agree with HOOKER's statement: "stipulis semicordatis petiolo sublongioribus," which is the case in no. 7; and HOOKER's diagnosis seems to me only explicable if we presume that he mixed two different forms. On the same sheet with no. 6 is also an old fruiting catkin with a leafy peduncle which is identical with those of no. 7. I am not yet sure to what species the sterile branch of no. 6 really belongs.

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[2] There is, however, a specimen, consisting of 3 leaves only, in herb. N. labeled "*Salix leucodendron* D. Don, in Pursh's Canadian Herb. (collected in Lord Selkirk's Exped. from Mr. Lambert's Herb.)." DON did not publish a species *S. leucodendron*, and I am not yet sure to which species these 3 leaves belong. PURSH's herbarium was in possession of LAMBERT (see Gard. Chron. 1842, p. 439), but PURSH himself did not collect in Canada at all (see HARSHBERGER, Bot. Philad. 115. 1899). I have not been able to get any information on "Lord Selkirk's Exped."

HOOKER also described a var. "*β. acutifolia;* foliis magis acutis vel subacuminatis," collected by RICHARDSON at Fort Franklin on the Mackenzie River, of which a photograph of the type "no. 76. Hb. H.B. and T." is before me. It consists of 3 pieces of young female flowering branchlets. I also saw a sheet with the label "no. 58. Hb. H. B. & T." ex herb. Torrey (N.) marked "Fort Franklin, Richardson," which contains 2 fruiting and 1 sterile branchlet of var. *acutifolia* named by RYDBERG *S. villosa* and marked no. 2. Besides these there are 2 sterile branchlets which may belong to var. *glabrescens;* the upper middle one was referred by RYDBERG to *S. villosa*, while the small one at the left corner of the lower label is without number. Furthermore, there are 3 sterile branchlets numbered 1 and named *S. chlorophylla* by RYDBERG which indeed look very much like this species or may be referable to *S. pulchra* Cham. All the specimens are referred (by BARRATT?) to *S. planifolia* Pursh, a very uncertain species which may be identical with *S. chlorophylla* And.

As already mentioned, ANDERSSON regarded HOOKER'S *S. villosa* in 1858 as only a variety of *S. glauca* L. He said: "Haec forma speciei maxime vegeta videtur," and in his short description (in Öfv. K. Vet.-Akad. Förh. **15**:109) we read: "foliis tenuioribus, supra (sic!) glaucis, sparse pilosis, elevato-venosis, stipulis subpersistentibus lanceolato-linearibus; amentis sat longis erectis laxiusculis, subrarifloris . . . ." The same diagnosis is repeated in Sal. Bor.-Am. 22, and in Walp., Ann. Bot. **5**:753. 1858. The statement "foliis supra glaucis" is certainly a misprint for "subtus glaucis," or it may be that a whole sentence has been omitted. Unfortunately, ANDERSSON did not cite a specimen, but his description scarcely fits the Rocky Mountain material collected by DRUMMOND. Ten years later ANDERSSON (in DC. Prodr. **16**^{2}:281) proposed a new hybrid *S. glaucops*,[3] which he placed without a number between 107. *S. glauca* and 108. *S. desertorum*, and of which he describes 2 "modifications," namely, var. *villosa*, being identical with his former *S. glauca* var. *villosa*, and var. *glabrescens*, which he based on specimens collected by BOURGEAU in the Rocky Mountains, and with which I shall deal later.

ANDERSSON referred to his *S. glaucops villosa* not only HOOKER'S *villosa* and his own *S. glauca villosa*, but also *S. villosa* Seemann ("Voy. of Herald. p. 39.54") and "*S. cordifolia* Hook. Fl. Boreal.

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[3] It ought to be mentioned that this species has been entirely misunderstood by M. J. JONES, Willow Fam. Great Plat. 16. 1908. The author says of his study: "This work, on western willows, is put forth tentatively in order to clear up doubts. . . . ." But he certainly succeeded in greatly augmenting the existing confusion in regard to many species. There are scarcely 2 willows better distinguished than *S. glaucops* And. and *S. subcoerulea* Pip., which JONES makes synonyms.

amer. p. 152. p.p. (non Pursh)." SEEMANN's plants came from western Eskimaux-Land (Northwestern Alaska from Norton Sound to Point Barrow), while HOOKER's specimens to which ANDERSSON alludes were collected in Labrador. The Rocky Mountain specimens mentioned by HOOKER are not included, as they had already been described by ANDERSSON as *S. subcordata* (*S. arctica* var. *subcordata* Schn., see my first paper). ANDERSSON's main description of *S. glaucops* fits best Seemann's specimens, and such forms as *S. villosa acutifolia* Hook., of which ANDERSSON made no mention at all either in 1858 or in 1868. According to the rules of nomenclature the name *S. glaucops* has to be applied to the *S. glauca* of Alaska, the Yukon, and the Mackenzie district if further investigations should prove that these forms can be regarded as a distinct species. Unfortunately, this name has been used by RYDBERG (1899) and BALL (1909) to designate a more southern form of the Rockies, for which I use the name *S. pseudolapponum* v. Seem. (see later). When BALL first treated this form in 1899 (Trans. Acad. Sci. St. Louis **9**:88) he expressly said: "Our Rocky Mt. form was included under *S. glauca villosa* by Mr. BEBB, but it is certainly not the *S. villosa* Don described by HOOKER (Fl. Bor.-Am. **2**:144) and later published by ANDERSSON as *S. glauca villosa* (Sal. Bor.-Am. 22). That had long leaves and thick aments 2–3 inches long, being thus more closely related to the European *S. glauca*." and (*l.c.* 89) BALL designates *S. glauca* var. *villosa* And. (*S. villosa* Barr., *S. glaucops* And.) as a form of which "full discussion must be deferred until more abundant material is accessible." He adds that "HANSEN's no. 800, Fl. Sequoia Reg., 1892, is a plant which nearly answers the original description," but in my opinion HANSEN's specimen differs widely from it, and belongs to *S. californica* Bebb, a fact suggested by BALL himself.

According to RYDBERG (1899), *S. glauca* is "apparently rare in America, and probably confined to the extreme northeast portion." Nevertheless, he cites, besides specimens from western Greenland and Labrador, "Alaska: Nurkagak, 1881. McKay," meaning Nushagak in the Bristol Bay. This specimen is referred by COVILLE to *S. glauca*. Furthermore, in 1901, RYDBERG described a *S. Seemannii*, the type of which had been "collected at Dawson by R. S. WILLIAMS, June 11, 1899, a more mature specimen June 12. Also collected by SEEMANN on Chamisso Island, 1851, no. 1873, and Kotzebue Sound and Norton Sound, 1849, no. 1423." He accompanied his description with the following remarks: "SEEMANN's specimens, cited below, were named by HOOKER *S. glauca* var. *macrocarpa*, but the plant is neither *S. macrocarpa* of TRAUTVETTER nor that of NUTTALL; it is related to the former, but not to the latter. *S. macrocarpa* Trautv. (*S. glauca macrocarpa* Ledeb.) is described as having sessile stigmas and fuscous bracts; it probably does not occur in America." In the original description of *S. macrocarpa* Ledeb. apud TRAUTVETTER (in Nouv. Mém. Soc. Nat. Mosc. **2**:292. 1832) I fail to find the statement that the stigmas are sessile; this part of the diagnosis runs: "stylo basin usque bipartito, stigmatibus bifidis." TRAUTVETTER compares in detail *S. glauca* and *S. macrocarpa*, and attributes to the latter the following characters: "frutex pedalis prostratus," "folia majora, acuminata, juniora jam fere prorsus glabra," and "pedicellus interdum fere longitudine ovarii." The same statement is given for *S. glauca* β *macrocarpa* Trautvetter in LEDEBOUR, Fl. Alt. **4**:281. 1833. Judging by those characters the American form in question cannot be identified with this var. *macrocarpa*, but better agrees with what TRAUTVETTER (1832) regarded as typical *S. glauca*, and named *S. glauca* var. *microcarpa* Ledeb. in 1833. Here TRAUTVETTER says, after having given an ample description of the specimens from the Altai, "exemplaria altaicis simillima Cl. Eschscholtz legit ad Cap. Espenberg."

As already stated, it is difficult to decide at the present status of our knowledge of the Old World forms of *S. glauca* whether some of them are identical with the American forms. So far as I can judge by TRAUTVETTER's descriptions and the material I have seen from Asia, I am not convinced that the forms of Northwestern America can be regarded as representing the typical *S. glauca* or one of TRAUTVETTER's varieties. A keen and careful observer like COVILLE, in 1901, said: "There is a tendency among American willow students to exclude *Salix glauca* from the North American flora, but our Alaskan specimens show so close an agreement with some European material of this species that I am unwilling to separate them." He adds that he is not "able to find in the description [of *Seemannii*] a record of any characters that serve to distinguish the specimens assigned to the latter species from forms of *glauca* found in America and Europe." I agree with COVILLE that the North American forms are very similar to those of *S. glauca*, but they are in my opinion not fully identical with the typical *S. glauca* L. s. str., the characters of which I have already indicated. In looking over the copious and well collected American specimens before me, I hesitate to designate them as typical *S. glauca*, nor am I willing to regard them as a separate species until a closer study of this circumpolar willow has convinced me of one fact or the other. Those specimens exhibit a great degree of variability in the shape and size of the leaves, in the amount of pubescence, in the length of the aments, and in the characters of the flowers. As a whole they seem to differ from the typical *S. glauca* by the usually well developed stipules, by the longer pedicels of the fruits which normally are from one-half to twice longer than the gland, and by the tendency of the filaments to become almost glabrous. Judging by COVILLE's statement with regard to *S. reticulata*, that "in all the other Alaskan willows the filaments are glabrous throughout," I supposed that this fact might furnish a good character to separate specifically the American *S. glauca* from the European-Asiatic species, but a close investigation of all the male specimens at my disposal convinced me that the filaments are always more or less hairy at their base. Specimens like nos. 3369 or 3373 of TRELEASE and SAUNDERS, which apparently have entirely glabrous filaments, do not seem to be pure *S. glauca*, and the American form probably hybridizes with other willows as freely as does the European one.

If we regard the American *S. glauca* as a distinct variety, we have unfortunately to use the varietal name *acutifolia* given by HOOKER to his variety of *S. villosa*, because it antedates ANDERSSON's *S. glauca villosa* by almost 30 years, and apparently represents a rather extreme form with narrowly lanceolate leaves. I regard my determinations as rather provisional, and I am not convinced that my present limitation of the Northeastern American forms of *S. glauca* can be taken as a definite solution of this difficult question.

As previously stated, ANDERSSON also described a *S. glaucops* var. *glabrescens* from specimens collected by BOURGEAU in 1858, probably in Alberta, Rocky Mountains district, near the Bow River Pass. The description runs thus: "*β, glabrescens*, amentis crassis vulgo multifloris, foliis rigidioribus supra sparse pilosis demum glabris subtus sat intense glaucis." Furthermore he said: "quam autem *glabrescentem* appelavi longius distat et *S. chlorophyllam* (e typo *S. phylicifoliae*) non parum revocat, foliis glabris supra lucidis et nervosis subtus glaucis reticulatis, amentis multo brevius pedunculatis et capsulis distinctius pedicellatis. Ad *S. desertorum* manifestissimum praebet transitum." There is a specimen of BOURGEAU's in Herb. G. which, in my opinion, represents a co-type of ANDERSSON's variety. It bears the label of PALLISER's Expedition and is named "*S. glauca* L.×*pallida glabrata* And." ANDERSSON not infrequently changed a name in his publication after having marked the herbarium sheets in a different way. The specimen consists of 2 pieces of well fruiting branchlets. The aments measure up to 5:1.5 cm. and do not differ from typical var. *acutifolia* (syn. var. *villosa*) as collected by BOURGEAU and DRUMMOND in the Rockies. The co-type before me apparently represents a less glabrescent form, and it approaches much the other variety, with which it seems connected by a whole series of intermediate forms. The most glabrous ones I have seen were collected in the vicinity of Dawson, Yukon Territory. I deem it best to give the following characteristics and synonomy of the two varieties:

1. S. GLAUCA var. **acutifolia**, comb. nov.—*S. villosa* Barratt apud HOOKER, Fl. Bor.-Am. **2**:144. 1839, p.p.; SEEMANN, Bot. Voy. Herald 39 (Fl. W. Eskimaux Land). 1852.—*S. villosa* var. *acutifolia* Hook., Fl. *l.c.*—*S. glauca* var. *villosa* And. in Öfv. K. Vet.-Akad. Förh. **15**:127. 1858, p.p.—*S. glaucops* α *villosa* And. in DC. Prodr. **16**^{2}:281. 1868, p.p.—*S. glauca* Richardson in FRANKLIN, Narr. Jour. Polar Sea, Bot. App. 753. 1833, non L.; COVILLE in Proc. Wash. Acad. **3**:321. pl. 39. 1901.—?*S. glauca subarctica* Kjellman, Fanerog. Vest-Eskim. Land 51. 1883, in Nordenskiöld, Vega Exp. Vet. Takttag. **2**:51. 1883, non Ldstr.—*S. Seemannii* Rydbg. in Bull. N.Y. Bot. Gard. **2**:164. 1901.—*S. glauca*, var. *Seemanii* Ostenfeld in Vid.-Selsk. Skrift. I. Math.-Nat. Kl. 1909.

no. **8**:34 (Vasc. Pl. Arc. N. Am. Gjöa Exp. 1904–6). 1910.—Frutex erectus, 0.5–1.5 m. altus; ramuli novelli dense albo-sericeo-villosi vel villoso-tomentosi, hornotini vix vel paullo glabrescentes, annotini biennesque pl. m. purpureo-brunnei vel epidermide secedente flavo-cinereo-brunnei, sparse vel partim villosulo-tomentosi vel glabrati, interdum pl. m. nitiduli, circ. 2–3 mm. crassi, vetustiores similes, glabri, saepe castanei; gemmae ut videtur ovatae, ventre pl. m. applanatae, apice saepe rostratae, obtusae, initio dense pilosae, demum fere glabrae, purpureo-brunneae, 4–5 mm. longae. Folia adulta pl. m. chartacea vel papyracea, inferiora minora (vel pedunculorum) elliptica, obovato-oblonga, oblanceolata, vel obovalia, basi obtusa vel vulgo cuneata, apice obtusa ad subacuta vel subrotunda et apiculata, integerrima, minimis margine saepe tenuiter glanduloso-denticulatis exceptis circ. 2:0.8 ad 3.5–4:1.5 cm. magna, superiora majora late lanceolata vel oblanceolata, elliptico- vel obovato-oblonga, ovato- vel obovato-elliptica, apice obtusa vel acuta vel fere breviter subacuminata, basi obtusa vel vulgo subito vel sensim cuneata, 5:1.5 vel 4.5:2 ad 7:2.3 cm. magna, surculorum saepe late ovato- vel obovato-oblonga vel late elliptica, 7:3 ad 12:6.5 cm. magna, maxima interdum margine distincte breviter denticulata, superne novella adpresse sericeo-villosa, etiam adulta pl. m. villosula vel vulgo glabrescentia, ad costam marginemque tantum distinctius villosula, estomatifera, costa nervisque lateralibus planis vel subimpressis, nervillis satis indistinctis, subtus novella densius quam superne sericeo-villosa, etiam adulta pl. m. adpresse sericea vel villosula, valde discoloria, albescentia vel glaucescentia, costa flavescente nervisque lateralibus utrinque circ. 6–10 pl. m. elevatis, nervillis saltem in foliis adultis tenuiter prominulis. Petioli 3–12 mm., in surculis ad 2 cm., longi, superne sulcati, ut ramuli pilosi, vel dein glabrati, flavescentes. Stipulae ut videtur semper evolutae, in ramulis vegetis maximae, pl. m. lineari- ad semi-cordato-lanceolatae, rarius semiovato-rotundae, satis distincte glanduloso-denticulatae, ut folia pilosa, petiolo duplo breviores ad $\frac{1}{3}$ vel fere duplo longiores, maximae surculorum ad 3:1 cm. magnae. Amenta coetanea vel subserotina, pedunculos ut rami pilosos foliatos terminatia, satis longe cylindrica, sub anthesi vulgo densiflora, rhachide villosa;

mascula pedunculis 0.5 ad 1.5 cm. longis exceptis (2–)2.5–4 cm. longa et 0.8–1 cm. crassa; bracteae oblongae vel obovato-oblongae, apice obtusae vel rotundae, rarius acutiusculae, concolores et stramineae vel ut videtur saepius pl. m. bicolores, apice purpurascentes vel fuscescentes, utrinque villosae et apice pl. m. sericeo-villosae; stamina 2, filamenta libera (rariter ad basim paullo connata), basi vel fere ad medium pl. m. pilosa (an interdum glabra?), adulta bracteis duplo ad 2.5plo longiora; antherae ut videtur ellipsoideae, flavae vel initio roseae; glandulae vulgo 2, interdum dorsalis non visa; ventralis late ovato-rectangularis vel oblongo-conica, apice truncata vel apice incisa vel bi(–3)fida, quam bractea 2–2.5plo brevior; dorsalis vulgo distincte minor et angustior, integra; feminea sub anthesi vulgo 2–4:0.8–1 cm. magna, fructifera laxiora satis elongata 3.5 ad 7 cm. longa et circ. 1.5 cm. crassa, pedunculis 1–3 cm. longis exclusis; bracteae oblongae, obtusae, iis florum mascul. similes; ovaria sub anthesi ovoideo-oblonga, subsessilia vel pedicello glandula breviore suffulta, dense albo- vel griseo-villoso-tomentosa; styli distincti, subcrassi, integri vel apice bifidi vel fere bipartiti brachiis saepe divaricatis quam stigmata bifida oblonga vix vel circ. ½plo longiores; glandula 1, ventralis, pl. m. late ovato-rectangularis et integra vel bifida ad bipartita, bractea circ. duplo brevior; fructus maturi ellipsoideo-conici, ut ovaria vel laxius villosi, pedicello vulgo distincto glandulam interdum ½ (rarius 2plo) superante excluso (6–)7–8(–9) mm. longi, valvis apertis paullo recurvatis.

This variety seems closely connected with the following one by intermediate forms, although the extremes look rather different.

S. GLAUCA var. **glabrescens,** nov. comb.—*S. glaucops*, var. *glabrescens* And. in DC. Prodr. **16**^{2}:281. 1868.—*S. Austinae* Rydbg., Fl. Rocky Mts. 198. 1917, non Bebb, pro parte.—Frutex ut in var. *acutifolia* descriptus, ab ea signis sequentibus praecipue differt: ramuli novelli vulgo minus dense villosi, hornotini pl. m. glabrescentes, rarius ab initio fere glabri vel citissime glabri, annotini biennesque glabri vel sparse (saltem partim) pilosi, olivaceo-purpurascentes, pl. m. nitiduli; folia apice saepe magis acuta, margine (saltem inferiora) saepius sed satis obsolete denticulata, majora

obovato-elliptico-oblonga vel late elliptico-lanceolata ad 6–7:2–2.5 cm. magna, superne saepe ab initio glabra, vividius colorata, subtus novella tantum pl. m. dense villosa, citius quam in *acutifolia* glabrescentia, adulta fere glabra vel parce pilosa, albescentia; filamenta basi sparsius pilosa, bracteae florum satis glabrescentes; amenta fructifera in co-typo ad 5 cm. longa et 1.5 cm. crassa, basi vix laxiflora, sed vulgo satis variabilia et basi pl. m. laxiflora; fructus pl. m. glabriores vel basi glabri.

So far as I can see, the range of var. *glabrescens* extends through the Rockies of Alberta and British Columbia to the northwest corner of this state and adjacent Alaska northward into the Yukon Territory, in the vicinity of Dawson. It probably occurs also in Alaska and the eastern Northwest Territories together with var. *acutifolia*.

As mentioned in the synonymy, RYDBERG has used the name *S. Austinae* Bebb as the specific designation for *S. glaucops glabrescens* And., but he also determined forms of a different origin as *S. Austinae*. This species had been proposed by BEBB in Watson, Bot. Calif. **2**:88. 1879, but BEBB himself stated (in BOT. GAZ. **16**:106. 1891) that it forms a mixture of 3 species, including *S. Lemmonii* Bebb and *S. lasiolepis* Bth. The female piece only represented an apparently new willow, and it is described as having "sessile aments appearing before the leaves, with small early deciduous bracts, dark scales, clothed with silky hairs." I fail to see how the name given to such a different form can be applied to *S. glauca glabrescens* even if we raise this variety to a specific rank.

Before it is possible to define correctly a variety like *glabrescens* we have to become much better acquainted with *S. pseudolapponum*, the so-called *S. glaucops* of the Rocky Mountain floras.

A few words must be said about the "*glauca*" of northeastern arctic America and of Greenland. I have to take into consideration the willows of Greenland because the flora of (at least western) Greenland is essentially American, and the forms of Labrador and northeastern arctic Canada cannot be properly understood without elucidating those of Greenland. The best enumeration of Greenland's *Salix* has hitherto been given by LANGE in his Conspectus Fl. Green. pt. 1. 1880 and pt. 2. 1887. In 1880 he cites not less than 5 varieties under *S. glauca*, which I cannot interpret correctly without comparing the specimens LANGE had before him, which are preserved in the herbarium at Copenhagen. So far as I can judge by the figures and quotations cited by LANGE, none of those varieties seems to be identical with the typical *S. glauca* or any of the forms of Northeastern Canada. The specimens from Labrador and Greenland referred to *S. glauca* by RYDBERG do not belong to it or are at least very uncertain in their relationship. There is only one form before me which seems to be closely connected with the true *S. glauca*, and of this I shall say something under *S. anamesa*, after having discussed the types and relatives of *S. desertorum*, *S. pseudolapponum*, and *S. cordifolia*.

2. S. DESERTORUM Richardson, Bot. App. in Franklin, Narr. Jour. Polar Sea 753 (reprint p. 25). 1833; ed. 2.765 (reprint p. 37). 1833; HOOKER, Fl. Bor.-Am. **2**:151. 1839, pro parte; ANDERSSON in DC. Prodr. **16**^{2}:281. 1868, excl. var.; RYDBERG in Bull. N.Y. Bot. Gard. **1**:272. 1899; excl. specim. Drummond.; BALL in Trans. St. Louis Acad. Sci. **9**:85. 1899, pro parte.—*S. glauca* **S. desertorum* And. in Öfv. K. Vet.-Akad. Förh. 127. 1858.—This is one of the most misunderstood willows, and I am sorry to say that I have not yet been able to explain it sufficiently. The type was collected by RICHARDSON at old Fort Franklin on the Mackenzie River. I have before me a photograph and fragments of the type material preserved in the Hookerian Herbarium at Kew, which show that the specimens distributed by BARRATT under no. 70 are identical with it. Unfortunately all the specimens have only young flowers and leaves except a few fragments of a fruiting catkin of the previous year in the Kew specimen. HOOKER (1839) referred to *S. desertorum* also specimens collected by DRUMMOND, and BEBB (apud ROTHROCK in Wheeler, Rep. U.S. Geol. Surv. West of 100th merid. **6**:Bot. 241. 1878) apparently took DRUMMOND's no. 657 for the typical *S. desertorum*, as did BALL (1899) on BEBB's authority. RYDBERG (1899) said: "It is evident that Mr. BEBB did not exactly know the true *S. desertorum*," and he stated that it is DRUMMOND's no. 658 that "matches RICHARDSON's specimens exactly." Both of DRUMMOND's specimens are before me. There is no doubt that no. 657 belongs to *S. brachycarpa* Nutt. (*S. stricta* Rydbg.), but I am likewise convinced that no. 658 is not identical with RICHARDSON's type. This number consists of two young male and female branchlets, and it differs chiefly by the pubescence of the young parts (the lower surface of the leaves, etc.) which is

mixed with minute fulvous hairs, by the rather long pedicel of the young ovaries which is about twice as long as the gland, and by the absence of a dorsal gland in the male flowers. At present I am unable to determine this plant correctly, as we do not know much of the *Salix* of the regions where DRUMMOND[4] collected.

ANDERSSON first mentioned *S. desertorum* quasi as a subspecies of *S. glauca*, and he said: "Insignis sane est forma, in orbe vetere quantum scio, non crescens. . . . Transitus vero ad normalem *S. glaucam* non nunquam reperti; videtur itaque hujus modificatio frigida." In 1868 he kept *S. desertorum* as a species, and added the following varieties: *α. elata*, *β. stricta*, and *γ. fruticulosa*. The last two are, in my opinion, nothing but *S. brachycarpa* Nutt. The first is based on specimens collected by DRUMMOND in the Rockies, but no number is given. It is described as "frutex 4–5-pedalis, ramis subsimplicibus crassis rufescentibus, foliis basi subangustatis supra glabris venis modice impressis subtus demum glabrescentibus amentis semipollicem longis." This description rather fits the male pieces of DRUMMOND'S no. 660 in herb. G., while the female piece of this number can hardly be distinguished from *S. brachycarpa*. This male no. 660 is the only one of DRUMMOND'S specimens I have seen that may belong to the true *desertorum*. This seems to be a species confined to the northern parts of Alberta and the Northwest Territories, but the young types are not sufficient to give a correct idea of the species. There is another specimen, however, preserved in the Torrey herbarium at New York and labeled "*Salix desertorum* Fl. Bor. Am." It consists of 4 pieces; a fruiting branchlet in the upper left corner of the sheet, a female one underneath it, and 2 male pieces at the right hand. The fruiting branchlet is undoubtedly *S. brachycarpa*, while the male and female material may be identical with the true *S. desertorum*. The male branchlet seems to represent a late flowering stage, and it bears rather far advanced leaves, the largest of which measure up to 4 cm. in length and 12 mm. in width. They are narrowly elliptical, acute at both ends, finely puberulous on the midrib and on some of the veins above, and glaucescent and almost wholly glabrous beneath, with an entire, ciliated margin. To the true *S. desertorum* may also belong (at least partly) the following 2 specimens collected by J. W. TYRULL: Hudson Bay, west of Chesterfield Inlet, September 2, 1893 (no. 1711 O., f., fr.), and between Lake Athabaska and Chesterfield Inlet, July-August 1893 (no. 1712 O., m., f.). Both numbers consist of several small pieces apparently taken from different plants, and it is impossible to judge them properly.

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[4] According to J. MACOUN (Cat. Can. Pl. I. preface p. viii. 1883), DRUMMOND "explored the whole country from the Red and Assiniboine Rivers by the North Saskatchewan and Athabasca to the Rocky Mountains." He also "collected in the main range of the Rocky Mountains, between lat. 52–56°, and particularly in the part about the head of the Smoky River, a tributary of the Peace." Dr. J. M. MACOUN is spending the summer of this year in these regions and will probably bring back many of the forms collected by DRUMMOND from their original localities.

I think it best to give the following description of the type material, because I shall not be able to insert *S. desertorum* into the key. Frutex erectus sesquipedalis (fide RICHARDSON), habitu ut videtur *S. pseudolapponum* non absimilis; ramuli novelli satis dense, rarius laxius albo-sericeo-villosi, hornotini paullo glabrescentes, annotini subglabriores vel tantum partim pilosi, brunnescentes vel interdum ut vetustiores vulgo nondum perfecte glabri purpurascentes et nitiduli, adulti flavo-brunnei, epidermide griseo secedente obtecti; rami cinereo-badii vel nigrescentes; folia speciminum typicorum valde juvenilia vel vix semi-evoluta membranacea, elliptico-lanceolata vel obovato-lanceolata (ex auctore "exacte elliptica"), apice obtusa vel vulgo pl. m. acuta, basi subito vel sensim in petiolum angustata, superiora integerrima vel tantum versus basim parce et obsolete denticulata, infima fere circumcirca tenuiter glanduloso-subdenticulata, maxime evoluta ad 3:0.9 cm. magna; superne ab initio glabra vel sparse (ad costam densius) villosula, in sicco subnigrescentia, valde indistincte subinciso-nervata et reticulata, stomatibus (an semper?) instructa, subtus pl. m. discoloria, glaucescentia, pruinosa, magis (saltem inferiora) sericeo-villosa sed cito satis glabrescentia pilis adpressis difficile recognoscentibus (tardius evoluta ut videtur distinctius pilosa); petioli nondum satis evoluti, vix ad 5 mm. longi, laxe sericei; stipulae nullae vel vulgo pl.m. evolutae, minimae vel parvae, maximae lanceolatae, glanduloso-denticulatae, parce pilosae, petiolis circ. $\frac{1}{3}-\frac{1}{2}$ breviores; amenta coetanea vel subserotina, cylindrica, ramulos breves foliatos sub anthesi vix ad 1 cm. longos terminantia, rhachide villosa;

mascula 2–3.5 cm. longa et circ. 8 mm. crassa, densiflora; bracteae oblongae ad obovatae, apice obtusae rotundataeve, stramineae vel flavo-brunneae (vix fuscae), pl.m. laxe praesertim ad apicem sericeo-villosae vel distinctius sericeae, extus saepe glabrescentes; stamina 2 filamentis liberis basi pl.m. pilosis dein bracteis duplo superantibus; antherae flavae(?), ellipsoideae, satis parvae; glandulae 2, ventralis ovato-conica, apice truncata, interdum pl.m. bifida, bractea 2.5–3plo brevior, dorsalis minor, angustior, vulgo integra; feminea sub anthesi 1.5–3:0.7 cm. magna; bracteae ut in masculis, sed brevius villosae, vix sericeae; ovaria oblongo-ellipsoidea, albo-villoso-tomentosa, sessilia vel subsessilia, styli sub anthesi breves, stigmatibus brevibus oblongis bifidis vix longiores, integri vel apice breviter bifidi; glandula 1, elongato-conica, apice truncata vel subretusa, interdum leviter incrassata, bractea duplo brevior; fructus tantum pauci anni praeteriti ex herbario Kewensi visi ellipsoideo-conici, subrostrati, circ. 6.5 mm. longi, satis glabrescentes vel tantum basi pedicelloque quam glandula subduplo breviore pilosi.

3. S. PSEUDOLAPPONUM v. Seemen in Bot. Jahrb. 29. Beibl. **65**: 28. 1900; RYDBERG, Fl. Rocky Mts. 197. 1917.—*S. glauca villosa* Andersson in Öfv. K. Vet.-Akad. Förh. **15**:127. 1858, pro parte; BEBB in Coult., Man. Bot. Rocky Mts. 338. 1885, pro parte max.—*S. glaucops* Rydberg in Bull. N.Y. Bot. Gard. **1**:270. 1899, p.p.m.; BALL in Coult. and Nels., New Man. Rocky Mts. Bot. 135. 1909, p.p.m.—*S. desertorum* Ball in Trans. St. Louis Acad. Sci. **9**:85. 1899, pro parte.—*S. glauca* var. ? Ball, *l.c.* 88, p.p.—*S. Wolfii* var. *pseudolapponum* Jones, Willow Fam. 17. 1908, prob. tantum ex parte.—To understand this species it is necessary to compare the explanations given under *S. brachycarpa* and *S. desertorum*. As I have already explained under *S. glauca*, the names *S. glaucops* and *S. glauca villosa* And. cannot be used for those forms which are named *S. glaucops* by BALL and also by RYDBERG, who keeps *S. pseudolapponum* as a different species. In his *Flora Colorado* 93. 1906, he distinguished them in the key by the following characters: "Leaf-blades oblong or linear-oblong; bracts obovate; shrub depressed," *S. pseudolapponum*, and "leaf-blades oblanceolate or obovate-lanceolate; bracts oblong; shrub not depressed,"

S. glaucops. In his *Fl. Rocky Mts.* 190. 1917, he says the same and adds that the leaves are 2–3 cm. long in the first, while they measure 3–6 cm. in length in the second species. The largest leaves of *S. pseudolapponum* I have seen measured up to 5.5:1.8 cm., but usually they are not longer than 4–4.5 cm., and from about 1.5 to 2.2 cm. wide. RYDBERG apparently refers to his *glaucops* some forms which I do not regard as belonging to it, giving as the range "Alta.—N.M.—Utah—Calif.—Yukon," while he restricts *S. pseudolapponum* to Colorado. The type of this species (*Baker, Earle*, and *Tracy*, no. 300½, male) came from Mount Hesperus in the La Plata Mountains in southwestern Colorado, and represents a young flowering stage which naturally looks rather different from a fully developed specimen with old fruits. After having compared an extensive series of well collected specimens, I fail to see how it is possible to separate specifically this southern Colorado plant from the other forms in Colorado, where the species seems to have its headquarters, but the typical *S. pseudolapponum* may represent a dwarfed more alpine form of the so-called *S. glaucops*, which, therefore, should be distinguished as a new variety of *S. pseudolapponum*. There are several forms which otherwise seem to be identical but do not have stomata in the upper leaf epidermis, with which the typical *S. pseudolapponum* is always provided, differing in this respect from *S. brachycarpa* (see later). So far as I can judge by the copious material before me, these two species seem to hybridize rather freely, and I cannot explain certain forms in any other way. We need, however, a much more careful study of these forms in the field to decide the question whether these hybrids are common. From New Mexico I know *S. pseudolapponum* only in a somewhat uncertain sterile form from Taos County, Costilla Valley (leg. *E. O. Wooton*, September 4, 1914), and from Wyoming I saw no specimen but *Nelson's* no. 7831 from the Medicine Bow Mountains in Albany County. From farther northward I saw specimens from Teton County, Montana (leg. *C. S. Sargent* in 1883), and from Alberta, Sulphur Mountain, near Banff (leg. *A. Rehder*, August 8, 1904). Specimens from Lake County, Utah, need further observation, and I have seen nothing from Nevada, California, Oregon, or Washington which I can refer to this species. A more intimate acquaintance with the *Salix* flora of these regions may lead me to a different opinion, but I hesitate to refer any doubtful forms to a certain species as long as I do not yet know all the other willows that may occur in the locality. Different species may sometimes look very similar at a certain stage of their development, and it needs a long time and the most scrupulous observation to become familiar with the variation of such polymorphic plants as the willows usually are.

4. S. BRACHYCARPA Nutt., North Am. Sylva **1**:69. 1843; RYDBERG, Fl. Colorado, 95. 1906; Fl. Rocky Mts. 197. 1917; BALL in Coult. and Nelson, New Man. R. Mt. Bot. 135. 1909.—*S. desertorum* Andersson in DC. Prodr. **16**^{2}:281. 1868, saltem var. β et γ, non Richardson; BEBB apud ROTHROCK in Wheeler, Rep. U.S. Geog. Surv. west 100th Merid. **6**: Bot. 241. 1878; in Coulter, Man. Bot. R. Mts. 338. 1885, excl. var.; BALL in Trans. Acad. Sci. St. Louis **9**:85. 1899, pro parte.—*S. stricta* Rydbg. in Bull. N.Y. Bot. Gard. **1**:273. 1899; in Mem. N.Y. Bot. Gard. **1**:114 (Cat. Fl. Mont.). 1900.—The type of this graceful and well marked species was collected by NUTTALL in August 1818 "in the Rocky Mountain range, on the borders of the Bear River, a clear rapid brook cutting its way through basaltic dykes to the curious lake of Timpanagos, in New Mexico" (now the Great Salt Lake of Utah). No type specimen seems to be in existence, neither have I seen a plant from the type locality, but NUTTALL's ample and vivid description leaves no doubt as to the form of which he is speaking. ANDERSSON entirely misunderstood this species when (in 1867 and 1868) he added NUTTALL's name with ? as a synonym to his *S. longifolia argyrophylla angustissima*. ROWLEE (in Bull. Torr. Bot. Club **27**:248. 1900) seems to have been the first who reinstated NUTTALL's name for *S. stricta* (And.) Rydbg. As already stated, *S. brachycarpa* is apparently connected with *S. pseudolapponum* by intermediate forms, and in 1899, through his investigation of the Rocky Mountain material, BALL was led "to the conclusion that no rigid line can be drawn between the species as they are represented in that region." The extreme forms, he said, are widely divergent, but the numerous intermediates present an almost perfect gradation between these extremes. After all, this

is true only to a certain degree, and in my opinion the difficulty might be settled by regarding the intermediate forms as hybrids. Compared with each other, *S. brachycarpa* is distinguished by the denser and shorter, almost tomentose pubescence, the absence of stomata in the upper leaf epidermis, the shorter petioles, and the denser and shorter aments, especially the staminate with their minute globose anthers; while *S. pseudolapponum* seems to be well marked by the looser, almost a little silky-villose pubescence, the relatively longer petioles, the presence of more or less numerous stomata in the upper leaf surface, and by the somewhat looser male aments with rather stiff filaments and larger, more ellipsoid anthers. In the female aments the differences are often less obvious, and the differences given by BALL (1909) and by RYDBERG (1917) seem to me not borne out in fact.

I have seen no material of *S. brachycarpa* from Utah where the type had been collected. The species seems to be abundant in central Colorado from the Culebra Range in the south to the Medicine Bow Mountains in the north, and southern Wyoming, where it is frequently met with in the western part of the state and in or near the region of the Yellowstone Park, including northeastern Idaho and southern Montana. There is also a specimen before me from the Wallowa Mountains in southeastern Oregon (*Cusick*, no. 2298). From northern Montana its range extends in the Rockies to about 59° N. lat. and about 122° W. long., while in Alberta it occurs east of the Athabasca River through Saskatchewan to about 59° N. lat. I also have before me specimens from Churchill on the western shore of the Hudson Bay in Manitoba, and from the Gaspé Peninsula, which I am unable to separate even as a variety. At first sight the eastern forms seem to differ by the relatively shorter and broader leaves, the somewhat longer styles, and the longer ventral glands, but the same variations can be observed in western specimens. The form from Churchill (*J. M. Macoun*, no. 79156 O.), however, needs further observation. An uncertain form is represented by no. 74, Hb. H.B. and T. (fr.; N.), named *S. desertorum* var. *acutifolia*. It differs from the type by foliis subacutis ad 32:9 mm. magnis et praecipue amentis fructiferis satis laxifloris ad 3.5:1 cm. magnis.

Professor J. M. MACOUN, to whom I am indebted for much help, has collected in company with M. O. MOLTE a very interesting variety at Jasper Park, Alberta, on the low point running into the Athabasca River on the west side of the discharge of Beauvert Lake, July 30, 1917 (no. 95374, fr.; O.), which has glabrous or almost glabrous ovaries and fruits. It resembles *S. chlorolepis*, but the leaves of this species possess stomata in the upper surface which soon becomes glabrous, while in the western form the leaves are without stomata as in typical *S. brachycarpa* and have the same kind of pubescence. I also received a male specimen collected by J. M. MACOUN at the same place as the female type on July 23, 1918, and I am giving the following description of this variety for which I propose the name:

S. BRACHYCARPA var. **glabellicarpa,** nov. var.—Frutex ut videtur parvus, dense et breviter ut in var. *typica* ramosus; ramuli novelli vetustioresque ut in illa; folia conferta, anguste lanceolata, oblanceolata vel anguste elliptico-lanceolata, apice acuta vel subito apiculata, basi cuneata ad subrotunda, 7:2 ad 28:8 mm. magna, integerrima, sed infima pl.m. dense tenuiter glanduloso-denticulata, superne infimis exceptis pl.m. laxe villosula, vivide (?) viridia, estomatifera, costa rubescente vel flavescente subimpressa nervis vix visibilibus, subtus discoloria, glaucescentia, densius villosula vel inferiora initio magis sericea demum glabrescentia, costa prominente, nervis lateralibus utrinque ad 8 angulo acuto a costa abeuntibus vix vel paullo prominulis; petioli 1–3 mm. longi gemmis (an satis evolutis?) ad subduplo longiores; amenta pedunculo ad 5 mm. longo normaliter foliato suffulta; mascula circ. 8:5 mm. magna ceterum a typo non diversa; fructifera circ. 1:1 cm. magna, subglobosa; ovaria sessilia vel subsessilia, glabra vel ad apicem parce villosa, stylo integro, stigmatibus siccis parvis bifidis ad 2.5plo longiore coronata; glandula 1, ventralis, anguste ovato-conica, quam bractea obovata flavescens vel apice straminea utrinque laxe villosa subduplo brevior; fructus ovoideo-conici, 4–5 mm. longi, ut ovaria glabra vel apice sparse pilosa.

5. S. CHLOROLEPIS Fernald in Rhodora **7**:186. 1905, is a species peculiar to the Gaspé Peninsula, where it was detected in 1905 at the headquarters of Ruisseau du Diable on the famous Mount

Albert by *Fernald* and *Collins* (no. 59, m., f.; G., type). As FERNALD has already pointed out, it closely simulates in habit, bark, and foliage *S. brachycarpa*, but differs from it by its glabrous capsules and glabrous green bracts. There are, however, pubescent forms which look rather intermediate between *S. brachycarpa* and *S. chlorolepis*, and which have been taken for hybrids by FERNALD. The main difference between the two species is, in my opinion, found in the glabrousness of the filaments in *chlorolepis*, which are more or less pilose in *brachycarpa*, and in the presence of numerous stomata in the upper leaf epidermis of *S. chlorolepis*, while *S. brachycarpa* is entirely destitute of them. The pubescent form agrees well with typical *S. chlorolepis* in this respect, and cannot therefore be regarded as of hybrid origin; consequently I propose the following variety:

S. CHLOROLEPIS var. **antimima**,[5] var. nov.—*S. desertorum* Fernald in schedis, non Richardson.—A var. typica nonnisi differt ramulis foliisque novellis bracteis vulgo extus et ovariis omnino vel parte superiore pl.m. breviter cinereo-villosulis, foliis vulgo oblongioribus ad 3:1 cm. magnis etiam adultioribus subtus saepe sparse pilosis.

The following specimens have been examined: Quebec: Gaspé Peninsula, Mt. Albert, on wet serpentine slopes, July 23, 1906, *Fernald* and *Collins* (nos. 512, 512^a, f., 512^c, f., type, 512^b, f., 512^e, fr., 512^f, m.; G.); July 21, 1906, *Fernald* and *Collins* (nos. 518, m. paratype, 519, f; G.; no. 519 forma intermedia inter var. *typicam* et var. *antimimam* videtur et ab cl. FERNALD sub nomine *chlorolepis*×*desertorum* distributa est); ravine of cold brook, local, alt. 900 m., August 12, 1905, *Collins* and *Fernald* (no. 64, m., f.; A., N.; "ascending shrubs 3–6 dm. high"). There are indeed also some forms which have to be regarded as true hybrids between *S. chlorolepis* and *S. brachycarpa*. I shall deal with them on a later occasion.

6. S. NIPHOCLADA Rydberg in Bull. N.Y. Bot. Gard. **1**:272. 1899; COVILLE in Proc. Wash. Acad. Sc. **3**:322. *fig. 20.* 1901.—This species is still very little known. Its type was collected in 1892 by Miss E. TAYLOR in the Northwest Territories on the "Mackenzie River, at a point 30 miles north of the Arctic Circle." I did not see the type specimen, but the specimens mentioned by COVILLE (*F. Funston*, no. 185 and *E. A.* and *A. E. Prebble* no. 26),

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[5] Derived from ἀντίμιμος, closely resembling.

who identified them with the type. The first came from the mouth of the Porcupine River in eastern Alaska, while the second was found near the mouth of the Seal River, 40 miles northwest of Fort Churchill on the Hudson Bay. Through the kindness of Professor J. M. MACOUN I saw also a small specimen collected by *F. Johansen* at Icy Reef in northeastern Alaska in 1914 (no. 164 or 93794 O.), which agrees well with *Funston* no. 185. *S. niphoclada* is "apparently nearest related to *S. stricta*" (*S. brachycarpa*) as stated by RYDBERG, while COVILLE was of the opinion that "the nearest relative to the species among American willows is *S. glauca*." In some respects *S. niphoclada* seems to approach *S. desertorum*, which, however, is still too insufficiently known. The statement in RYDBERG's description, "style 5 mm. long," is clearly a misprint for 0.5 mm. Owing to the lack of more copious material I am unable to elucidate the genetic relations between *S. desertorum*, *S. niphoclada*, and *S. brachycarpa*, nor can I properly define the taxonomic characters of the first 2 species. The most significant character of *S. niphoclada* seems to me the dense white silky-villose pubescence of the first season's shoots combined with the very short and densely silky petioles, which apparently do not exceed 2 mm. in length, while they are about twice as long and more obvious in *S. desertorum*. I am not inclined, therefore, to refer *Seton* and *Prebble's* no. 79 (no. 78300 O.) from the Mackenzie district, Artillery Lake, Last woods, to *S. niphoclada*, as it has been determined by BALL, as it seems to me more closely related to *S. desertorum*. We know, however, almost nothing of the *Salix* flora of the woodland region of the Northwest Territories, which must be an Eldorado for willows.

The following species which I propose is likewise characterized by the very short petioles, but it has an entirely different prostrate habit.

7. **S. fullertonensis**, nov. spec.—Frutex humilis depressus ramis ramulisque vulgo satis elongatis repentibus, floriferis ut videtur tantum adscendentibus. Ramuli novelli pl.m. villosuli vel breviter sericeo-villosuli, hornotini pl.m. glabrescentes, purpureo-brunnescentes, annotini fere glabri vel partim tomentelli, intense brunnescentes vel fere castanei, interdum subnitiduli, vix ultra 2 mm.

crassi, vetustiores epidermide secedente griseo obtecti; rami pl.m. cinereo-brunnei. Gemmae parvae, oblongae, obtusae, ellipsoideae vel fere ovato-globosae, flavescentes vel purpurascentes, initio pilosae, ut videtur vix ultra 2.5 mm. longae. Folia satis parva, adulta sub-chartacea, lanceolata, ovato- vel elliptico-oblonga, interdum anguste ovato-elliptica, elliptica, ovalia vel obovato-oblonga, apice vulgo acuta, rarius obtusa, basi pleraque rotundata, interdum late cuneata, margine integerrima vel rarius basim versus dentibus distantibus minimis glanduliferis paucis instructa, 1:0.4 ad 2.5:0.9 cm. magna vel (in no. 79161) ad 3 cm. longa et ad 1.1 cm. lata, superne novella pl.m. villosula vel etiam adulta nondum glabra, rarius fere ab initio glabra, ut videtur intense sed satis obscure viridia, costa paulo impressa nervis lateralibus subplanis, epidermide (an semper?) stomatifera, margine villosulo-ciliata, subtus discoloria, albescentia vel glaucescentia, pruinosa, novella et etiam adulta ut superne sericeo-villosula vel demum fere glabra, costa flavescente elevata nervisque lateralibus utrinque 5–8 prominulis ceterum satis indistincte tenuiter reticulata; petioli brevissimi, gemmis duplo breviores ad aequilongi, superne sulcati, pilosi, basi dilatati, vix ultra 2 mm. longi; stipulae vulgo evolutae, semicordatae vel semiovato-lanceolatae, acutae, pl.m. glanduloso-denticulatae, pilosae, 1–3 mm. longae. Amenta tantum feminea saepius fructifera visa, pedunculis (0.5–)1–2 cm. longis foliatis suffulta, cylindrica, sublaxiflora, sub anthesi circ. 1.2–1.5:0.5 cm., fructifera 2:1 ad 4:1.3 cm. magna; ovaria ovoideo-conica, dense griseo-villoso-tomentosa, sessilia, stylo brevi semipartito vel integro quam stigmata oblonga subbreviore ad sublongiore coronata; bracteae anguste oblongae, obtusae (in no. 79161 obovali-oblongae), brunnescentes, villosulae vel sericeo-villosulae, extus ad apicem interdum glabrescentes; glandula 1, ventralis, anguste ovato-conica, apice truncata, integra vel pl.m. bifida bipartitave, quam bractea circ. duplo brevior, in no. 79161 interdum glandula dorsalis parva visa; fructus anguste ovoideo-conici, ut ovaria vel minus dense tomentosi, sessiles vel subsessiles, 4–6 (vel ad 7) mm. longi.

TYPE LOCALITY: Eastern Canada, Hudson Bay, Fullerton, lat. 63°57′.

SPECIMENS EXAMINED: Canada: Hudson Bay, Fullerton, September 4, 1910, *J. M. Macoun* (79164, fr.; type; G., N., O.); July 10, 1904, *E. L. Borden*

(no. 63043, f.; N., O.; a young flowering stage); Ranken Inlet, lat. 62°45', August 30, 1910, *J. M. Macoun* (nos. 79163, 79165, 79166, fr.; Cor., N., O.; identical with type); Bathurst Inlet, Arctic Sound, lat. 67° to 68° N., long. 109° to 111° W., August 25, 1915, *R. M. Anderson* (no. 467 or 93776 O., fr. im.; amentis satis laxifloris); Cape Eskimo, lat. 61° 05', August 26, 1910, *J. M. Macoun* (no. 79161, fr.; Cor., N., O.; forma foliis fructibusque majoribus, saltem in specim. in O., stomata superne in foliis ut videtur deficientibus); Mansfield Island, September 1884, *R. Bell* (no. 24622, fr.; O.; specimen mancum incertum).

This is an interesting willow, and well marked in its typical form by the very short petioles of the small leaves, which are normally provided with stomata in the upper surface. It seems to be an entirely prostrate shrub with very slender creeping branches. Some of the forms I regard as *S. fullertonensis* or nearly related to it have been referred by RYDBERG to his *S. Macounii*, the type of which represents a very different plant, which I shall discuss under *S. cordifolia*.

The following specimens look to me more or less like forms that might be taken for *S. fullertonensis*×*S. groenlandica.* They seem to differ from *S. fullertonensis* in the following characters: gemmis majoribus ad 5:3 mm. magnis, foliis latioribus ovato- vel obovato-ellipticis ovalibus vel obovato-oblongis apice saepe plicato, acutis basi rotundis ad late cuneatis adultis margine sparse ciliato excepto glabris superne magis nitidulo-viridibus (stomatiferis) subtus paullo distinctius nervatis reticulatisque maximis ad 2.8:1.5 cm. magnis; petiolis ad 4 mm. longis sed gemmas bene evolutas non superantibus; amentis fructiferis fructibusque vix diversis, bracteis late obovatis pl.m. longius et magis sericeo-pilosis; fructibus sessilibus vel pedicello distincto glandulam interdum superante suffultis, circ. 7 mm. longis.

Hudson Bay: lat. 55–56°, barren shores, August 1886, *J. M. Macoun* (no. 18822, fr.; O.; ovariis sessilibus, bracteis sericeis, foliis distincte petiolatis, stomatiferis); Fullerton, September 4, 1910, *J. M. Macoun* (no. 79148 fr.; O.; 79167, fr.; Cor., G., N., O.; forma foliorum ut in *fullertonensi* sed petioli longiores, stomata desunt, ovaria subsessilia, glandulae saepe 2, bracteae sericeae); Ranken Inlet, lat. 62°45', August 30, 1910; *J. M. Macoun* (no. 79162, fr.; Cor., G., N., O.; *S. groenlandicae* satis similis); Nottingham Island, 1884, *R. Bell* (no. 18820[1] olim, = 54358 O., fr. juv.; satis ad *anglorum* spectans sed sine stomata); Digges Island, 1884, *R. Bell* (no. 18820[3] olim, = 54359 O.; fragmentum, ut praecedens); Mansfield Island, 1884, *R. Bell* (no. 18820[5] olim, = 54360 O.; fr.; probabiliter ut praecedens); James Bay mouth of Albany

River, July 25, 1904. *W. Spreadborough* (no. 62618, fr.; O.; magis ad *groenlandicam* spectat); Bathurst Inlet, Katur Point, lat. 67° to 68° N., long. 100° to 111° W., August 22, 1915, *R. M. Anderson* (no. 456 or 93775 O., f.; specimen mancum).

7. S. Cordifolia Pursh, Fl. Am. Sept. **2**:611. 1814; Trautvetter in Nouv. Mém. Soc. Imp. Nat. Mosc. **2**:298. *pl. 9* (De Salic. frig. Kochii). 1832; Hooker, Fl. Bor.-Am. **2**:152. 1839, exclud. specim. Drummond.—*S. callicarpaea* Trautv., *l.c.* 295, *pl. 7;* Rydberg in Bull. N.Y. Bot. Gard. **1**:270. 1899, quoad specim. labrad.—*S. planifolia* Hook., *l.c.* 150, quoad specim. labrad. saltem ex parte, probabiliter non Pursh.—*S. alpestris* c) *americana* Andersson in Öfv. K. Vet.-Akad. Förh. **15**:129. 1858.—*S. arctica β Brownei* 3° *fumosa* And. in DC. Prodr. **16**^{2}:287. 1868, quoad pl. labr.—*S. glauca* Rydbg. in Bull. *l.c.* 271, quoad pl. labr.—*S. Wag-hornei* Rydbg., *l.c.*, pro parte; Britton and Brown, Ill. Fl. ed. 2. **1**:604. *fig. 1486.* 1913.—*S. labradorica* Rydbg., *l.c.* 274, pro parte max.—Pursh's description of this species is very short and runs as follows: "*S.* depressa; foliis ovalibus subacutis basi cordatis integerrimis reticulato-venosis supra glabris, subtus pallidis nervo margineque pilosis, stipulis semicordatis." It was taken from a sterile plant cultivated "in Hort. Andersson." Pursh adds "in general habit it resembles *S. myrsinites.*" Unfortunately there is no type left by Pursh, but a specimen from Andersson's garden is preserved at Kew, of which I have not yet seen a photograph, but only a rough outline sketch in herb. G. The plant is next mentioned by Forbes (Salict. Wob. 277. *fig. 143.* 1829), who only translated Pursh's diagnosis. The leaf represented in *fig. 143* clearly shows a finely denticulate margin, and it looks much more like a leaf of *S. calcicola* Fern. I am unable to ascertain its identity. Hooker said: "The plant named for me by Mr. Borrer, who is probably acquainted with the original plant cultivated by Andersson, little deserves the appellation of *cordifolia*, its leaves being more frequently acute than retuse at the base. Many of the specimens approach very near the following" (*S. arctica* R. Br.). I have not yet seen the Labrador type of Hooker's *cordifolia* collected by Kohlmeister. Hooker also referred to this species specimens collected in the Rockies by Drummond which represent *S. arctica*

subcordata (And.) Schn. (see my first paper). In the synonymy he mentioned *S. obovata* Pursh with a ?, but this species is described with "amentis subcoetaneis sessilibus" and does not apparently belong to our species. Furthermore, HOOKER'S *S. planifolia* is the same as *S. cordifolia* as to Miss BRENTON'S specimens from Labrador, of which I have a photograph and fragments before me. The sheet in herb. K. contains 6 specimens with fruits and adult female flowers of which only one (the middle piece at the left hand side) seems to belong to a different form on account of the presence of stomata in the upper leaf surface which are wanting in typical *S. cordifolia*.

Judging by the ample descriptions and the figures, TRAUTVETTER'S *S. cordifolia* and *S. callicarpaea* seem to represent nothing but two different stages of one species. His *S. cordifolia* is a poor specimen of a female plant with young flowers, while the figure of his *callicarpaea* shows a fruiting specimen collected by HERZBERG at Okak. Of RYDBERG'S *S. callicarpaea* I have only seen BELL'S Labrador specimen from "Nachhak" (Nachvak), a rather poor and sterile one (no. 18819, O.) which I cannot distinguish from typical *S. cordifolia*.

The other specimen cited by RYDBERG from Mt. Gaspé (probably meaning Mount Albert, Gaspé Peninsula), collected in 1882 by *Macoun* (no. 18826 O.), has not been available to me; it may belong to *S. anglorum* var. *kophophylla* Schn.

ANDERSSON (1858) divided *S. cordifolia* Hook. in his *S. subcordata* and *S. alpestris americana*, the latter representing the Labrador plant. In the *Prodromus* (1868) no mention is made of his *alpestris* and its 3 varieties of 1858, but only of the older *S. alpestris* Wulfen, which has nothing to do with it. *S. cordifolia* is cited under *S. arctica* β *Brownei* f. 1. *obovata* in the following sentence: "Huc *S. cordifolia* Pursh fl. 2. p. 611; Hook. fl. boreali-amer. 2. 152; Trautv. *l.c.* p. 298 t. 9 ex Labrador forsan etiam pertinet"; while on the following page under f. 3. *fumosa* of the same variety he says "Nonne haec potissimum: *S. cordifolia* Pursh fl. Amer. syt. 2.611. ?, Trautv. *l.c.* p. 298 (quae tamen stylo longissimo insignis videtur!)", and *S. callicarpaea* Trautv. is mentioned as a quasi-synonym under the last form. Besides this ANDERSSON says under *S. pyrenaica:*

"*S. cordifolia americana*, quam olim *S. Pyrenaicae* forma credidimus, vix a formis foliis tenuioribus nigricantibus *S. villosae* est distinguenda." This is a most curious statement, because he never referred *S. cordifolia* (or part of it) to *S. pyrenaica*, but he did propose (1858) a *S. alpestris α pyrenaica* besides his *alpestris americana*. Furthermore, under *S. glaucops* var. *villosa* ANDERSSON (1868) quotes "*S. cordifolia* Hook. Fl. Boreal.-amer. p. 152 p.p. (non Pursh)." These statements convey the impression that ANDERSSON was unable to interpret properly HOOKER's species.

RYDBERG (1899) proposed the new name *S. Waghornei* for *S. cordifolia* Hook., not Pursh, without explaining why both are not identical, and without mentioning the fact that HOOKER in his *cordifolia* also included specimens of DRUMMOND from the "high parts of the Rocky Mountains." He says "Type in Herb. Torrey ('Fl. Am. Bor.')," which is a poor and almost valueless fragment consisting of one piece with a few remnants of fruits and another small one with undeveloped rather abnormal male catkins. The leaves of both have stomata in the upper epidermis, and the specimen looks more like a hybrid between *S. cordifolia* and *S. anglorum* than like *S. cordifolia*, which is certainly not identical with this "type." I am inclined therefore to use the name *S. Waghornei* for this supposed hybrid.

RYDBERG (1899) proposed 2 more species: *S. atra* and *S. labradorica*. Judging by the type before me, *S. atra* represents nothing but a form of *S. cordifolia*, of which I shall speak later, while *S. labradorica* is still a rather uncertain form because the female type (*Waghorn's* no. 36, 1892) as well as the male syntype (*Waghorn's* no. 31, 1892) differ from typical *S. cordifolia* by the presence of stomata in the upper leaf epidermis. The plants are too young to afford sufficient characters to recognize their real affinity. According to RYDBERG's key, *S. labradorica* differs from the other species by its broadly ovate leaves "with white, villous almost permanent hairs, spreading in all directions," while in *S. Waghornei* and *S. atra* "the leaves are somewhat hairy when young, but the long white hairs are, as in *S. glauca*, appressed and parallel to the midrib." This kind of silky pubescence may be seen on the lower surface of the first (lowermost) leaves of almost all the forms in question, while the later (superior) leaves bear more or less villous hairs "spreading in all directions," especially on the upper surface if the latter is not glabrous even when young, as is mostly the case with the young (first) leaves of the flowering branchlets. I have been unable to distinguish different forms by the amount or the character of the pubescence, and it is often difficult to determine properly young flowering specimens in the herbarium.

S. cordifolia is a widely distributed and variable species, its range extending from southern Greenland (about the 67th parallel) and Labrador (from the vicinity of Nachvak southward to the Strait of Belle Isle) westward to the western shores of the Hudson Bay (in var. *atra*) and southward to the Mingan Islands and the western Gaspé Peninsula,[6] northwestern Newfoundland, and in var. *Macounii* to the Bonne Bay region in western Newfoundland, but it is not yet reported from the Bay of Islands or the Blomidon range there. The forms of Greenland which I take for *S. cordifolia* are discussed under *S. anamesa*.

In Labrador it is often represented by the f. **atra** (Rydbg.), nov. forma, which seems to differ from the type only in its more oblong leaves which are acuter at both ends. The "turning black in drying" of the leaves mentioned by RYDBERG seems to me no character of taxonomic value because it is too often only a result of neglect in the press. I shall give an enumeration of the specimens referable to f. *atra* in my final book. At present I wish to draw the attention of collectors to another form for which I propose the name f. **hypoprionota**[7] nov. forma, because it chiefly differs from the type by its "foliis ex parte pl.m. serrato-denticulatis"; otherwise it seems to vary in the same manner as the type, being sometimes more or less prostrate, sometimes an erect shrub up to 1 m. in height. I refer to it the following specimens:

LABRADOR: Straits of Belle Isle: Blanc Sablon, limestone and calcareous sandstone terraces, by brook, August 1, 1910, *Fernald* and *Wiegand* (nos.

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[6] There is a specimen from Mt. Albert collected August 27, 1882, by *Macoun* (no. 24500 O., with old male aments and mature leaves) which closely simulates the western *S. glauca* var. *acutifolia* from Alberta, and I cannot distinguish another of MACOUN's specimens of August 2, 1882, said to be collected in "Gaspé, Que." with ripe fruits from the western *S. glauca*. But this has no number and I do not feel quite sure of the locality.

[7] Derived from *ὑπό*, somewhat, and *πριονωτός*, serrated.

3224, f.; G.; foliis elliptico-oblongis paullo ad *f. atram* spectans; 3226 fr. type; G., "shrub 1 m. high"; foliis obovato-ellipticis ad 5.8:3 cm. magnis superne magis quam subtus laxe adpresse villosis vel inferioribus minoribus margine ciliato excepto glabris); Forteau, springy banks and damp hillsides, July 10, 1910, *Fernald* and *Wiegand* (nos. 3210, 3220, fr.; G.); Fox Harbor, near Battle Harbor, September 15, 1891, *Waghorne* (no. 11ᵃ, fr.; Cor.); Ungava, along a river, July 1896, *Spreadborough* (no. 13687ᵃ O.; Cor.); Quebec: Mingan Islands, Ile St. Géneviève, July 1, 1915, *H. St. John* (no. 90840 O., m., f.; G.); Island of Anticosti, Baie Sainte Claire, August 17–18, 1917, *M. Victorin* (nos. 4349, st., 4350, st., 4351, fr.; A.).

A distinct variety seems to be represented by the typical *S. Macounii* Rydbg., which came from Ellis Bay on Anticosti Island. Rydberg referred to this species forms of different origin, but mostly those related to *S. fullertonensis* and *S. groenlandica*. It may be briefly characterized as follows:

7b. S. cordifolia var. **Macounii**, nov. var.—*S. Macounii* Rydbg. in Bull. N.Y. Bot. Gard. **1**: 269. 1899, quoad specim. typic. —*S. Rydbergi*[3] Heller, Cat. N. Am. Pl. ed. 2. 4. 1900.—*S. vacciniformis* Rydbg. in Britton, Man. Fl. N. St. Can. 319. 1901.—A typo praecipue differt foliis etiam adultis minoribus vix ultra 3:1.5 cm. magnis vulgo satis exacte ellipticis utrinque pl.m. acutis interdum margine pl.m. denticulatis adultis glaberrimis sed novellis pl.m. (saltem superne!) ut in typo villosis; amentis fructiferis vix ultra 3:1 cm. magnis.

Type locality: Island of Anticosti, Ellis Bay.

Range: Anticosti and northwestern Newfoundland, possibly also in Labrador and northern Ungava.

Specimens examined: Quebec: Anticosti, Ellis Bay, September 7, 1883, *J. Macoun* (no. 18830 O., fr.; type).—Newfoundland: Ingornachoix Bay, damp rocky limestone barrens, near the sea level, August 4, 1910, *Fernald* and *Wiegand* (nos. 3203, f., fr., 3207, fr.; G.); dry rocky limestone barrens, near sea level, August 1, 1910, *Fernald* and *Wiegand* (no. 3218, fr.; G.; prostrate); August 2, 1910, *Fernald* and *Wiegand* (no. 3221, f., fr.; G.); Bonne Bay, barrens at the base of the serpentine table lands, August 27, 1910, *Fernald* and *Wiegand* (no. 3229, f.; G.); serpentine table land, alt. about 380 m., same date and collectors (no. 3230, fr.; G.).

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[3] There is no reason according to the international rules or the Philadelphia code to change the name *Macounii* on account of the previous *S. Richardsonii* var. *Macouniana* Bebb, as Heller in November 1900 and Rydberg a few months later did, the latter not knowing of Heller's name.

This variety needs further observation. It seems to be the prevailing one on Anticosti Island and in northwestern Newfoundland. Some more vigorous forms from Blanc Sablon and Forteau with more distinctly denticulate leaves might also be referable to it. RYDBERG's type is a very glabrous specimen collected in September. Forms from Hopedale in Labrador (*Sornborger*, no. extra 1) and northern Ungava (*A. P. Low*, no. 24769 O.) are rather uncertain. Specimens like no. 3207 have the mature leaves entirely glabrous (except a few hairs on the margin), as in the type, while the young parts show a more copious pubescence similar to that of *S. cordifolia typica*.

There are other specimens which I cannot determine properly and which are worth further observation:

Newfoundland: Ingornachoix Bay, Pointe Riche, limestone barrens near sea level, August 4, 1910, *Fernald* and *Wiegand* (no. 3204, fr.; G.), forma foliis pl.m. orbicularibus vel elliptico-rotundis satis ad var. *Macounii* spectans, fere ut in var. *typica* pilosa, sed floribus femineis glandula satis lata (fere ut in *groenlandica*) instructis et fructibus pedicello quam glandula sublongiore suffultis laxe puberulis, stylis brevibus stigmatibus brevibus bifidis vix longioribus, bracteis obovatis substramineis breviter pilosis.—Quebec: Saguenay County, Archipel Ouapitagone, Ile Matchiatik, sprawling on ledge, July 15, 1915, *H. St. John* (no. 90841 O., f.; G.), praecedente non absimilis.

A very uncertain form has been found by *St. John* on the Mingan Islands, Ile au Marteau (Eskimo Island), top of limestone shingle, July 28, 1915 (no. 90837 O., m., f.; G.): ramulis novellis perspicue dense albo-tomentosis, foliis semi-evolutis obovato-ellipticis ad 5:2.5 cm. magnis costa ex parte petioloque excepto glabris superne in epidermide stomatiferis inferioribus ut in f. *hypoprionota* denticulatis, stipulis semiovatis denticulatis glabris, floribus ut in *S. cordifolia* sed bracteis apice interdum leviter fuscis.

Lastly, there remains to be discussed a willow from western Greenland which seems most closely related to *S. cordifolia*, but which also considerably resembles *S. anglorum*, and has apparently been referred by most of the authors to *S. glauca*. I cannot include it among any of the species previously mentioned, but deem it best to propose a new species.

9. **S. anamesa**,[9] spec. nova.—Frutex ut videtur habitu variabili ut in *S. cordifolia;* ramuli novelli dense sericeo-villosi, hornotini

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[9] Derived from ἀνάμεσος, intermediate.

pl.m. glabrescentes, autumno ut annotini vulgo partim pilosi, badii vel purpurascentes, etiam vetustiores saepe vix omnino glabri, dein nigro-purpurascentes vel epidermide secedente pl.m. cinereo flavescentes, ad circ. 5 mm. crassi. Gemmae ovato-oblongae, obtusiusculae, initio dense pilosae, dein glabrescentes, purpurascentes, petiolis duplo breviores. Folia adulta ut videtur papyracea, elliptica, elliptico-oblonga, ovali-elliptica vel elliptico-obovata, minima interdum anguste elliptico-lanceolata vel oblanceolata, margine integerrima vel rarius parva dentibus minimis sparsis glandulosis sub pilis occultis instructa (in no. 156 etiam majora distinctius sparse denticulata), maxima nondum perfecte evoluta ramulorum typi ad 2.5:1 cm. magna, in speciminibus a cl. Hartz in Augusto lectis ad 3.5:1.5 cm. magna et in ramulo vegeto (in no. 156) ad 4.8:2.3 cm. vel in forma satis incerta a Disco Island ad 5:2 cm. magna, superne ut videtur obscure viridia, in sicco vulgo pl.m. nigricantia, novella inferiora adpresse sericea, superiora pl.m. (praesertim versus marginem) villosula, adulta satis glabrescentia sed in costa pl.m. pilosula et margine ciliato-villosa, in epidermide pl.m. (saltem secundum nervos) stomatifera, subtus valde discoloria, glaucescentia, inferiora et novella dense sericea vel sericeo-villosa (pilis adpressis albis vel paullo flavescentibus), demum glabriora et adulta interdum tantum sparse pilosa, costa nervisque lateralibus 6–10 prominulis flavescentibus et laxe tenuiter reticulata. Petioli initio dense, dein sparse sericeo-villosi, superne sulcati, 2–5(–6) mm. longi. Stipulae breviter ovatae vel ovato-lanceolatae, acutae, denticulatae, ut folia colorata et pilosa, 1–3 mm. longa vel nulla (punctiformia). Amenta coetanea, ramulos breves dense sericeo-villosos foliatos sub anthesi vix ultra 12 mm. longos terminantia, cylindrica, rhachide sericeo-villosa; mascula 1.2–3:1 cm. magna, basi saepe sublaxiflora; bracteae oblongae, obtusae vel subobtusae, stramineae vel apice paullo fuscescentes, omnino sericeo-villosae et apice magis sericeae; stamina 2, filamenta libera, circ. $\frac{1}{3}$ pilosa, bracteis dein duplo longiora; antherae ellipsoideae, mediocres, violaceae (tantum juvenilia?), glandulae 2, ventralis anguste conica, apice truncata, integra vel pl.m. bipartita, dorsalis minor, angustior; feminea 1–2:0.8–0.9 cm., fructifera ut videtur ad 4:1.5 cm. (Hartz, Holstenborg) magna, basi vix distincte laxiflora; bracteae ut in masculis, saepe brevius pilosae, omnino stramineae;

ovaria ovoideo-oblonga, dense albo-villoso-tomentosa, subsessilia; styli distincti, bifidi vel bipartiti (brachiis saepe divaricatis) stigmatibus brevibus oblongis bifidis haud vel ad duplo breviores; glandula 1, ventralis, ut in masculis, bractea circ. duplo brevior. Fructus ovoideo-conici, ut videtur ad 8–9 mm. longi, minus dense quam ovaria villosi, subsessiles.

TYPE LOCALITY: South Greenland, Ilua, lat. bor. 59°55′.

RANGE: Southern and western Greenland.

SPECIMENS EXAMINED: Greenland: Ilua, lat. bor. 59°55′, May 15–31, 1889, *E. L. Lundholm* (m., f., type; M.); Sermiliarsuk, circ. 61°30′, August 3, 1889, *N. Hartz* (fr.; N.); Kingua Kuanersok, circ. 62°, July 12, 1889, *N. Hartz* (m.; N.); Kvanefjord S. f. Frederickshaab, 1886, *L. K. Rosenvinge* (no. 18873 O., fr.; needs further observation); Godthaabs district, Kobbefjord, June 28, 1884, *Warming* and *Holm* (m., f.; G.); Holstenborg, June 14, 1889, *N. Hartz* (f., fr. adult.; N.); Disco Island, Godthaab (probably mistake for Godthavn!), July 14, 1892, *W. E. Meehan* (no. 62 or 24768 O., m.; ramulis magis glabrescentibus annotinis fere glabris lucido-purpureis, forma porro observanda); Godthavn, August 2, 1896, *Cornell Party* (m., f.; Cor.; forma ut videtur prostrata aspectu *S. anglorum* non absimilis sed characteribus florum ab *S. anamesa typica* non diversa); Nugsuak Peninsula, Camp 2, August 10, 1896, *Cornell Party* (fr.; Cor.; forma porro observanda, bracteis magis obovatis, fructibus breviter pedicellatis, foliis apice saepe subito breviter plicato-acuminatis); Wilcox Head, August 15, 1896, *Cornell Party* (f., fr.; Cor.; forma porro observanda, amentis fructiferis ad 4.5:1.4 cm. magnis, fructibus pedicello quam glandula vix breviore suffultis, foliis ad 4:2 cm. magnis pl. m. obovato-ellipticis); Camp 3, August 20, 1896, *Cornell Party* (f.; Cor.; forma foliis satis breviter petiolatis ceterum paullo ad *S. anglorum* accedens); Upernivik, 72°47′, July 18, 1886, *L. K. Rosenvinge* (no. 24514 O., f.; looks very much like *S. cordifolia* but the pubescence reminds more of *S. anglorum;* on July 24 the same collector found a specimen at Pröven which I cannot distinguish from *S. anglorum*); Cape York, July 23, 1894, *E. H. Wetherill* (no. 214; G.; specimen mancum dubium tantum amentis fructiferis adultis praeditum habitu valde ad *S. anglorum* spectans sed bracteis breviter villosis oblongis); Omenak (Umanak) Fjord, Omenak Island, August 9, 1897, *D. White* and *Ch. Schuchert* (no. 156, fr.; N.; forma porro observanda, foliis ad 4.5:2 magnis, amentis fructiferis ad 3.5 cm. longis et 1.6 cm. crassis).

As already said, this species is certainly most closely related to *S. cordifolia*, from which it chiefly differs by the presence of stomata in the upper leaf surface. I should have treated it as a variety of this species were it not for the fact that there are a number of quasi intermediate forms between it and *S. anglorum*. On the other

hand, *S. anamesa* is not identical with *S. Waghornei*, which I take for a hybrid between *S. anglorum* and *S. cordifolia*. I have not yet seen any *S. anglorum* south of Disco Island in Greenland, and the Greenland material which I am inclined to refer to *S. cordifolia* is very scanty and needs further observation. From *S. anglorum* the new species may at once be distinguished by its hairy filaments and its narrowly oblong, light brown bracts, which have the rather short and villous pubescence of the *cordifolia* type. It seems to me that *S. anamesa* represents the plant commonly called *S. glauca* by LANGE, HARTZ, and other authors, but I am not sufficiently acquainted with the *Salix* of Greenland, owing to the scarcity of material from there in American herbaria, to give a more proper definition of the so-called *S. glauca* and the numerous varieties of it described by ANDERSSON, LANGE, and others. I do not find in the existing literature a name I could apply to *S. anamesa*. The *Salix* of Greenland seem always to have been compared only with those of Europe, while in fact the material before me indicates a much closer relationship with the species from Northeastern America. If we glance at the varieties of *S. glauca* mentioned from Greenland, we find the following in LANGE's Consp. Fl. Groenland. **1**:110. 1880, and **2**:279. 1887:

S. glauca var. *sericea* And., the type of which is *S. sericea* Vill., Hist. Pl. Dauph. **1**:382. 1786, nom. nud.; **3**:782. *pl. 51. fig. 27.* 1789, and which ANDERSSON refers to his f. 3. *lanceolata*. According to LANGE (1880) this var. *sericea* and also var. *appendiculata* (Vahl) Wahlb. are "tolerably common on some moist places." The latter variety is well figured by VAHL, Fl. Dan. 6. fasc. **18**:6. *pl. 1056.* 1792. Neither of these varieties seems to me identical with the forms I refer to *S. anamesa*. LANGE's third variety, var. *ovalifolia* Lge., Fl. Dan. 17, fasc. **50**:11. *pl. 2981.* 1880 (*S. glauca α sericea 2 ovalifolia* And.; ?*S. glauca* var. Brown in Trans. Bot. Soc. Edinbgh. **9**:450. 1868) pro parte, may be represented by the following 2 specimens before me: Disco Island, September 1854, *Lyall* (fr.; N., ex Herb. Hook.), and "Gebiet des Umanakfjordes (70–71° N.Br.)," August 18, 1892, *E. Vanhöffen* (no. 89[220], fr.; N.). The broad-elliptic or oval leaves which measure up to 3.5:2.3 or 5: 2.2 cm., and are more or less villous, especially on the rib of the upper surface and on the margin, do not have stomata in the upper epidermis, and their villous petioles are hardly 5 mm. long. Some of the leaves, especially in no. 89, show a few fine distant teeth toward the base. The branchlets of the season are covered with rather long villous hairs, while the older ones become glabrous and of a shining dark purplish color. The fruiting aments measure up to 4.5 by 1.5 cm., and the capsules are about 10 mm. long, including the very short pedicels. The habit of the plant cannot clearly be recognized, but there is another very similar fruiting specimen collected by *H. E. Wetherill*, at Netiulene, Whale Sound, North Greenland, August 13, 1894 (no. 226; G.), which certainly is taken from a prostrate plant. This number is enumerated by RYDBERG (1899) under *S. anglorum*, but it lacks the stomata in the upper epidermis, and seems more closely connected with the var. *ovalifolia*, being however a little more glabrescent than the other 2 specimens mentioned. The sessile capsules are about 8 mm. long, and the bracts somewhat darker.

The var. *angustifolia* Lange, Fl. Dan. 17. fasc. **50**:11. *pl. 2982*. 1880, is a very striking narrow-leaved form, the type of which came from Iceland ("prope Myvatu Islandiae legit cl. Lundgren"). I much doubt if it is the same as *S. glauca α sericea 4 angustifolia* And. (1868). LANGE (Consp. Fl. Gr. **1**:110) refers to it specimens from western and eastern Greenland which I have had no opportunity to compare. The only specimen I saw which somewhat resembles LANGE's plate is *Wetherill's* no. 225 from the north side of the Jones Sound, August 1894 (f.; G.), but here the leaves have stomata in the upper epidermis and the rather silky pubescence of the dark bracts points more to *S. anglorum*, of which it may be a narrow-leaved form. I have seen rather similar specimens of *S. anglorum* from southwestern Victoria Land (*R. M. Anderson*) and northeastern Greenland (*A. Lundager*).

LANGE's last var. *alpina* (not *S. glauca δ alpina* And., which is the same as *S. glauca β macrocarpa* Ledeb.) is described as a "fruticulus humilis, repens vel prostratus, ramis adscendentibus, foliis minutis, raro ultra ½ poll. longis," and as the type there has to be taken a specimen collected by *R. Brown* (of Campster) in 1867 at Jakobshavn in western Greenland (*S. glauca* Brown in Trans. Bot.

Soc. Edinbgh **9**:430. 1868, pro parte). I have seen nothing identical with this variety; there is only one specimen before me from the "Kvanefjord S. f. Frederickshaab," collected in 1886 by *L. K. Rosenvinge* (no. 18873 O., fr.) which I should take for a small-leaved form of *S. anamesa*, the narrowly elliptical leaves measuring up to 21:9 mm.

I can only repeat that we have to make a much closer investigation of the so-called *S. glauca* of Greenland in order to decide which of the forms can really be referred to the European species. They are certainly not identical with the var. *acutifolia* and var. *glabrescens* previously mentioned. I strongly believe that the true *S. glauca* is entirely absent from Eastern North America, and here represented by *S. cordifolia* and its varieties. It is the main purpose of these explanations to call attention to what is still unknown of the difficult forms of this group of willows, of which the following remains to be discussed.

10. S. LINGULATA Andersson in DC. Prodr. **16**²:281. 1868; Herder in Act. Hort. Bot. Petrop. **11**:437. 1891.—This is a very poorly known Alaskan species not mentioned by COVILLE. ANDERSSON described it from specimens collected by *Kostalsky* "ad Alaxa" as a low shrub resembling in habit a small *S. arbuscula*. There are a few fragments in herb. N. ex Herb. Fischer which agree well with ANDERSSON's description (except that the leaves are not quite glabrous above), but are much too scanty to give a distinct impression of this species. The flowers, etc., suggest those of *S. desertorum*, and *S. lingulata* is certainly closely connected with the species of the GLAUCAE with pilose filaments, but has nothing in common with *S. reticulata*, to which it is said by ANDERSSON "capsulis globoso-ovalibus . . . . sat evidenter referrens."

ARNOLD ARBORETUM
JAMAICA PLAIN, MASS.

THE SPORANGIA OF THISMIA AMERICANA

NORMA E. PFEIFFER

(WITH PLATE XVI)

Of the investigations among Burmanniaceae, the morphological studies of TREUB, JOHOW, and ERNST and BERNARD are prominent. These studies included both chlorophyllous and dependent forms, although the latter are better represented. The accounts vary considerably in completeness, since in the earlier ones close stages are sometimes lacking.

That there is variety within the family in development up to the mature seed is evidenced in the widely different accounts for those forms in which there is no evidence of fertilization, as compared with those where this process undoubtedly occurs. The net product seems to be approximately the same, that is, a small mass of endosperm cells about an embryo of from 2–10 or more cells, usually with no differentiation. A striking exception occurs in *Thismia clandestina*, which has a 3-celled suspensor and a spherical body differentiated into 2 layers. As in Orchidaceae (**12**), however, the preliminaries to this vary. Division of the megaspore mother cell may produce a row of 2 cells (as *Burmannia candida*, **5**), in which the inner cell gives rise to the embryo sac; or a row of 3 cells, the innermost of which, a true megaspore, functions in producing the female gametophyte; or the usual tetrad of angiosperms, of which the innermost megaspore is functional.

In the production of these cells the mother cell may go through a reduction division (as *Burmannia Championii*, **5**), in which case fertilization is the rule; or it may divide by an ordinary mitotic division, so that the progeny have the double number of chromosomes rather than the reduced number (*Burmannia coelestis*, **2**).

In all cases the embryo sac mother cell, whether a megaspore or the result of a single division of the archesporial cell, develops by 3 consecutive divisions to produce the 8-celled stage. Polarity is early evident, and the egg apparatus is organized, with small antipodal cells at the opposite end of the sac, while the 2 polar nuclei usually meet near the center, sometimes nearer the chalazal or micropylar end (as *Burmannia Championii*, **5**).

When the egg is mature, in some cases there is evidence of the entrance of a pollen tube with the discharge of two male cells, one of which fuses with the egg, the other with the polar nuclei, as *B. candida*. That the latter fusion is not a complete one is held by ERNST and BERNARD, who see in a 3-parted nucleus with 3 nucleoli evidence against entire merging, at least in the first divisions of this endosperm nucleus. The fusion of the egg nucleus, however, is slower here than that of the 3 nuclei in the center of the sac. When there are 2–4 cells in the endosperm, the sex nuclei still remain distinct in *B. candida* (**5**). Later the fertilized egg gives rise to an embryo of 2 or more cells, varying with the form studied.

In cases where no fertilization has been observed there was development of seeds as indicated, except that no fusion save that of the polar nuclei occurred. *Thismia javanica* (**3**) and *Burmannia coelestis* (**2**), examples in which this condition holds, show no reduction division in the formation of the "megaspore." This condition is the one to be expected from such work as has been done in parthenogenetic angiosperms. The development of the seed is first evidenced in *B. coelestis* by the division of the endosperm nucleus, which usually results from the fusion of 2 polar nuclei; occasionally there are more than the two concerned, as 3–5, probably through the functioning of synergids or antipodal cells. Thereafter the development seems much as in sacs where fertilization has taken place. ERNST and BERNARD in their series of studies of Burmanniaceae report for *B. coelestis*, *B. candida*, *B. Championii*, *Thismia clandestina*, *T. Versteegii*, and *T. javanica*, practically the same sort of development in the endosperm region, regardless of the introduction of a male cell. The first division of the fusion nucleus gives rise to 2 nuclei, the lower of which is cut off by a wall. The cell thus formed is designated as the "basal apparat" or haustorium cell. The other nucleus, however, continues to go through successive divisions in which no cell plate is formed, with the result that there are a number of free nuclei in the endosperm region. Walls then develop in this region at approximately the same time or a little before the beginning of nuclear division in the embryo cell proper. The extent of tissue development in *B. Championii* may be judged by ERNST and BERNARD's statement that there are 6–8 cells in the median longitudinal line in the mature sac, and that *B. coelestis* has about 30 endosperm cells at maturity.

The antipodal cells, never conspicuous, usually appear in a little V-shaped region below the haustorium region, sometimes as a row of cells, more frequently as two cells above one.

The cell giving rise to the embryo, whether after fertilization or not, goes through at least one nuclear division, and usually more. *Gonyanthes candida*, as reported by TREUB (**13**), develops a 2-celled embryo; as reported by JOHOW, and again by ERNST and BERNARD (as *B. candida*), it has a 3-celled embryo. JOHOW (**8**) found in *Gymnosiphon tenellus* a 3-celled situation similar to B. *candida*, and in *Dictyostegia orobanchioides* and *Apteria setacea* a 4-celled embryo, comparable to that found in *B. javanica* by TREUB (**13**). *Gymnosiphon trinitatis* (**8**) and *Thismia javanica* (**3**) show slightly greater development in a 6 or more-celled embryo, whereas *Thismia clandestina* (**4**) shows the greatest differentiation in a structure consisting of a 3-celled suspensor and a spherical body in which a single outermost layer of cells is differentiated from the inner mass. There is a striking similarity to Orchidaceae (**12**) so far as extent of development of the embryo is concerned. The contrast in the mature seed, on the other hand, due to failure of endosperm development in Orchidaceae, is equally noticeable. JOHOW, and later ERNST and BERNARD, have described the development of a small "nucellus polster" above the embryo sac, and an even more conspicuous tissue at the chalazal end. The possibility of the functioning of the latter at the time of germination of the seed as a region of water transfer (the rest of the tissue shows great cutinization) has been suggested, although no evidence of experimental character has been forthcoming. In contrast to the striking nucellus tissue at the ends, there is very evident degeneration of the cells in the middle zone or ring, as in *Gymnosiphon*, *Burmannia candida*, and *Thismia clandestina*.

In comparison with the thorough work done on embryo sacs, the scant attention paid to the pollen situation brings forth practically only the method of pollination and fertilization where this process occurs. This has been reported by several workers: MIERS (**9**) in *Dictyostegia orobanchioides*, WARMING on Brazilian forms and in *Apteria lilacina*, and ERNST and BERNARD in *Burmannia candida* and *B. Championii*. In all these forms germination of pollen occurs in the pollen sacs, so that the tufts or bundles of pollen tubes issue from the anthers and penetrate the stigma. MIERS remarked that the identity of these pollen tubes is clear with the use of a common lens, while the cottony mass of threads is evident, supposedly to the naked eye. He distinctly stated that this is not true, however, in *Myostoma* and *Ophiomeris* (**9**), and took this as evidence, in his early time, that thereby "the theory of the application of pollen tubes for the fertilization of its ovules is distinctly disproved." ERNST and BERNARD were unable to discover this method of pollination in *Thismia javanica* or *T. clandestina*, although aware of its presence in other forms and so alert for indications here. So far the evidence goes to show that such early germination of pollen and subsequent growth occur only in Euburmanniae, where the structure of the flower is different from that in *Thismia*. There seems to be a general conclusion, however, that forms are self-pollinated, through evidence such as given by SCHLECHTER in *Thismia Winkleri* (**1, 11**), where little diptera were found in the base of the flower where the pollen must fall.

Investigation

The material upon which the present study is based is that of *Thismia americana*, collected by the writer in Chicago, Illinois, during the summers of 1913 and 1914. The relationships of this form and a description of its structure, etc., were given in a previous paper (**10**).

In very young stages the stamen set appears to be distinct earlier than the ovary parts. Each stamen, of which there are 6, produces the usual 4 microsporangia, all of which are directed away from the central axis of the flower. Thus the surface of the anther toward the center is quite flat or slightly concave, while the opposite one is marked by the 4 lobes, in 2 pairs, which represent the rudiments of the microsporangia. At this stage usually the connectives have not become so broadened as later, so that the individual stamens appear more distinct than the tube shows at maturity. The youngest stage where differentiation appears is indicated in fig. 14, where hypodermal masses of meristematic cells, separated from each other by a double layer of sterile cells, appear beneath a distinct, large-celled epidermal layer. At this time the ovary chamber is just beginning to show distinctly with the 3 placentae, which later give rise to the ovules projecting inward. Later the individual sporangia show the parietal layer to be but 2 layers thick, within which there is a conspicuous tapetum, while outside of it is the epidermal layer (fig. 15). The tapetum shows dark irregular bodies which may represent waste or reserve material. At this stage it is evident in many preparations that not all of the tissue originally differentiated as "sporogenous" is fertile. A number of the spores abort, so that in any one section only a few appear normal (fig. 16). Often between adjacent cells small oil globules appear as extraneous matter, possibly released through changes due to degeneration of the spores.

The microspores are shed from the stamens through a longitudinal dehiscence of the anther. At the time of shedding one division of the microspore nucleus has taken place in such as appear functional. The tube and generative nuclei can be distinguished quite readily, although often other bits of dark staining material are present.

Germination of pollen grains with formation of fine pollen tubes has been observed. By dissection of the style several tubes were traced through to the ovary cavity. At this time practically all the pollen had been shed from the stamens of the flowers under consideration. It seems likely that there is self-pollination as in other forms. The contrast with the Euburmannia forms reported lies in failure of development of the mass of pollen tubes from the microsporangia to the stigma, as reported by MIERS and ERNST and BERNARD. The structure would practically bar such a possibility, since the greatly developed stamen tube arising from the connectives usually extends below the level of the stigma. The dehiscence of the microsporangia occurs on the face away from the central region in which the style is erected, and the pollen falling from the sacs would naturally drop to the floor of the cavity, that is, the roof of the ovary. In this fall it is obvious that the grains cannot come in contact with the stigma, which is separated by the stamen tube, although grains have been observed along the style. The cells of the inner surface of the stamen tube are often glandular in nature (fig. 16), although this would seem to have no special significance except in connection with the entrance of insects. It seems likely that the latter are necessary agents in pollination because of the mechanics involved.

The placentae which appear in the ovary during the development of the microsporangia give rise after a time to the primordia of the ovules (fig. 1). The surface of the placentae first becomes uneven through the appearance of the little lobes marking the rudiments. Soon the inner integument appears, and finally, as the ovule assumes the anatropous orientation, the outer integument is quite distinct except on the side where the funiculus appears. Meanwhile the hypodermal archesporial cell has become differentiated (fig. 2). The condition of mother cells usually occurs in the stamens at the same time that this archesporium appears in the ovule (cf. figs. 2 and 15). This cell represents the megaspore mother cell directly, since no parietal cells are developed here. It enlarges noticeably, and at length undergoes nuclear division, during which the chromatic material becomes massed at one side of the nucleus in synapsis (fig. 2). After division two cells separated by a thin wall are evident (fig. 3). At the same time the whole ovule is developing rapidly, as shown by the spindles in the tissue about the megaspore mother cell or its progeny. The two daughter cells divide further. The spindle in the outermost cell is oriented at right angles to the long axis of the ovule, that of the inner parallel to this axis. The result is that there is a pair of megaspores side by side which frequently are so crushed together in later stages that they lie obliquely (fig. 5) or appear finally as one (fig. 10). Sooner or later these cells disorganize, as does the sister cell of the functional megaspore, which lies innermost in the series of four. The pressure of development usually shows first on the outermost megaspores (fig. 5), but sometimes the third non-functional one is crushed first (fig. 6).

At the time of the first division of the megaspore developing the gametophyte, the abortive cells are dark staining, often wholly disintegrated masses of material. The binucleate stage shows nothing unusual, with its tendency toward polarity with the appearance of a central vacuole (figs. 8, 9). This stage is followed by the usual 4-nucleate situation arising from the division of each of the nuclei (fig. 10). The 4-nucleate phase must give rise very soon after formation to the 8-nucleate, since it represents a difficult stage to find.

The early 8-nucleate stages (fig. 11) show 4 free nuclei at each pole, with a large central vacuole. This is followed by great enlargement and the organization into an embryo sac of the typical form of angiosperms, the egg apparatus at the micropylar end consisting of 2 large synergids in contact with the egg, 3 smaller free antipodal nuclei in the narrower, more pointed chalazal end of the sac, and 2 polar nuclei, usually coming in contact with each other near the micropylar rather than the chalazal end (**12**). Stages both before and after the fusion of these polar nuclei have been found. The peculiar lobed effect reported by ERNST and BERNARD in *Burmannia candida* and interpreted there as incomplete fusion is sometimes evident here. That there is any special significance here seems doubtful.

At this time the cells surrounding the embryo sac stain more deeply and stand out more sharply than in younger stages. So far fertilization stages have not been observed. Contrary to ERNST's report of development in *Burmannia coelestis*, it seems altogether likely that fertilization does occur, since pollen tubes are developed.

The development of the seed has not been followed in detail. At one time the larger portion of the sac is filled with the free nuclei resulting from the division of the endosperm nucleus. Soon walls come in, forming large cells. At about this time the egg cell undergoes division, so that a 2-celled proembryo is present imbedded in the conspicuous endosperm tissue. Further division occurs in the proembryo cells; and in the oldest material obtained (presumably mature seeds, although not so proved by germination) the embryo consists of many cells in a globular mass with a short suspensor region (fig. 13). The situation is much like that in

Thismia clandestina. The endosperm is packed with reserve material at this time, and stains very deeply as a result.

The development of the nucellus and integument into peculiar layers has been noted under the literature of other forms. In *Thismia americana* there is also at maturity a distinct mass of irregular small cells at the base connecting by means of a dark staining nucellar layer with a cap of peculiar cells at the micropylar end. The nucellar layer next to the endosperm shows fungal hyphae and many oil bodies as part of the contents. Gelatinization of the walls at the chalazal end begins early, and is responsible to some extent for the prominence of the mass of cells at that end.

Enough material has not been available to try a satisfactorily large range of germination experiments. Those which have been tested have given negative results. In all probability, as in orchids, the fungus plays a rôle in the early development of the plant.

Summary

1. In the microsporangia the sporogenous cells develop from hypodermal masses, 4 in number, in the usual fashion.

2. At maturity the innermost parietal layer appears crushed by the large tapetal cells.

3. There is marked abortion of sporogenous cells in the microsporangia.

4. The division of the megaspore mother cells gives rise to 4 megaspores, the outer 2 oriented at right angles to the long axis of the ovule.

5. The 3 outer megaspores degenerate very soon, disappearing entirely after a short time.

6. The functional megaspore divides in the usual way, so that eventually an embryo sac of 8 nuclei is produced.

7. Presence of pollen tubes makes fertilization seem likely.

8. The well developed embryo is imbedded in large endosperm cells which are conspicuous in storage contents.

9. In the seed the nucellus makes a conspicuous layer, developing into a cap of tissue at each end.

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EXPLANATION OF PLATE XVI

All figures were drawn with the aid of the camera lucida, and show magnifications as follows: figs. 1, 3, 5, 10, ×840; 13, 14, 15, 16, ×500; 17, ×260; 2, 7, 8, 9, 11, ×916; 4, 6, ×784; 12, ×1651.

Fig. 1.—Primordium of ovule.

Fig. 2.—Synapsis in megaspore mother cell.

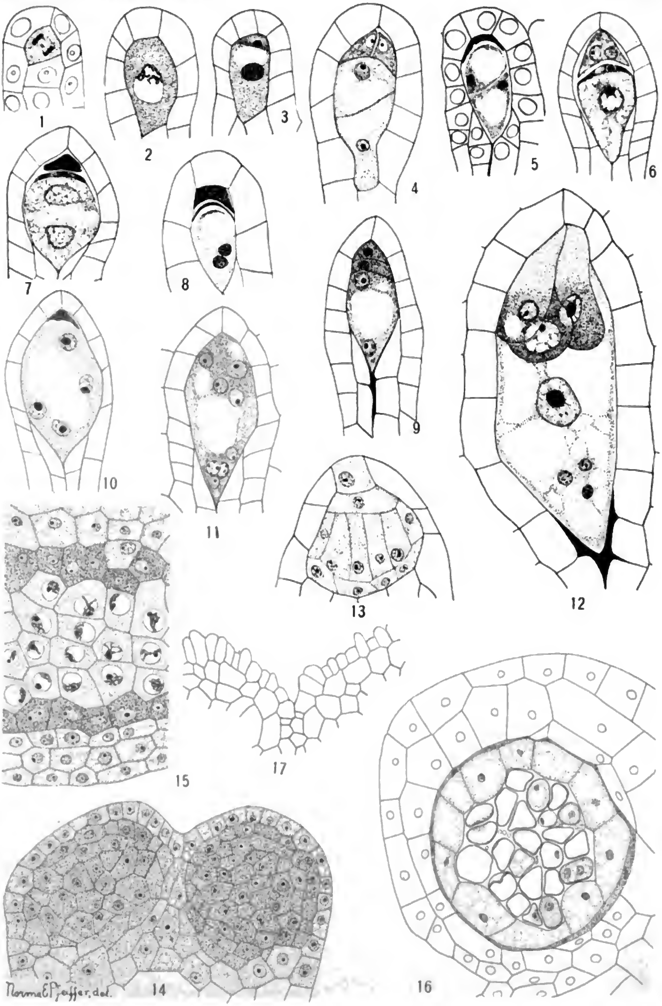
Fig. 3.—Daughter cells of megaspore mother cell.

Fig. 4.—Four megaspores.

Fig. 5.—Four megaspores, two outer cells already disorganized.

Fig. 6.—Same stage, but sister cell to functional megaspore crushed.

Figs. 7–9.—Binucleate embryo sacs.



PFEIFFER on THISMIA

FIG. 10.—Four-nucleate embryo sac; non-functional megaspores disorganized.

FIG. 11.—Eight-nucleate embryo sac.

FIG. 12.—Embryo sac at maturity; chalazal walls conspicuously gelatinized.

FIG. 13.—Embryo.

FIG. 14.—Young anther, showing 2 of 4 microsporangia.

FIG. 15.—Microsporangium with mother cells in synapsis, longitudinal section.

FIG. 16.—Microsporangium, showing large number of sterile pollen grains, tapetum disorganizing.

FIG. 17.—Portion of stamen tube, showing glandular cells of inner surface (nearest style).

ROOT VARIATIONS INDUCED BY CARBON DIOXIDE GAS ADDITIONS TO SOIL[1]

H. A. NOYES, J. F. TROST, AND L. YODER

(WITH NINE FIGURES)

Under discussions of tropisms in plants it has been customary to include statements relative to the tropic influences of gases on plant roots. Primary investigations on this subject were made by MOLISCH,[2] using seedlings of *Pisum sativum* and *Zea Mays*. Gases were caused to flow past the roots of the plants, and tropic curvatures were reported for all the gases employed. BENNETT[3] repeated these experiments and concluded that the results obtained were hydrotropic. BENNETT made further studies with *Zea Mays*, *Raphanus sativus*, *Cucurbita Pepo*, *Pisum sativum*, and *Lupinus albus*, both in artificial and in so-called natural media. Studies made with the seedling roots in air gave no indication of aërotropism. Studies made in earth, when the sprouted seedlings were placed between blotting papers in pots of moist earth and then subjected to streams of carbon dioxide gas for periods varying from 24 to 60 hours, gave no definite curvatures.

CANNON and FREE,[4] after working with *Prosopis veluntia*, *Opuntia versicolor*, *Fouquieria*, *Coleus Blumei*, *Heliotropium peruvianum*, *Nerium oleander*, and *Salix* (probably *S. nigra*), concluded that "it seems probable that soil aëration must be added as a factor of no less importance than temperature and water," for these plants were found to have different responses to carbon dioxide added to soil. The following quotation is self-explanatory.

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[1] Contribution from Research Chemistry and Bacteriology Laboratories of Department of Horticulture, Purdue University Agricultural Experiment Station, Lafayette, Indiana.

[2] MOLISCH, H., Über die Ablenkung der Wurzeln von ihrer normalen Wachthumsrichtung durch Gase (Aërotropismus). Sitzungsber. Akad. Wiss. Wien.

[3] BENNETT, MARY E., Are roots aërotropic? BOT. GAZ. 37:241–259. 1904.

[4] CANNON, W. A., and FREE, E. E., The ecological significance of soil aëration. Science N.S. 45: 1017.

The ecological bearing of these facts is manifest. Although deficiency in aëration has frequently been suggested as an agricultural difficulty, or as the reason why certain species do not grow upon soils of heavy texture, it does not appear that this suggestion has had any exact experimental basis, nor does it seem to have been appreciated that different species may have great differences in the oxygen requirement of their roots and widely variant responses to differences in soil aëration, responses which appear to be quite as specific and significant as the responses to temperature and to available water which forms the present basis of ecological classification.

One of the writers[5] reported 2 preliminary experiments with *Zea Mays* and *Lycopersicum esculentum.* Flower pots containing these species were kept surrounded by an atmosphere of carbon dioxide. Practically all the aërial portions of the plants were in normal atmosphere. The plants responded differently to the gas during and subsequent to the 2 weeks' treatment given.

This paper is a report of experiments in which carbon dioxide gas was introduced subterraneously into soil in Wagner pots. Experiments will be reported following up the work of CANNON and FREE, in which the plants will be grown in soil sealed away from the air, so that there is no chance for the oxygen of the air to diffuse down into the soil. Studies on the effects of aëration on bacterial activities have convinced the writers that unless the soil worked with was sterile (which would be unnatural) or contained known organisms of known antagonisms and activities, the responses to changed conditions of aëration might be due to a cessation of certain necessary biological activities, or to the occurrence of certain detrimental biological activities. Adding carbon dioxide gas to the soil was expected to change the biochemical activities of the soil, but by having the atmosphere come in direct contact with the surface, it was believed that necessary biochemical activities could exist, although perhaps closer to the surface than normally. The surface of the soil of all pots was left normal (dust mulch), so that all conditions might more nearly approximate those present when the carbon dioxide content of the soil was increased by natural means. Differences in amount, nature, and type of root growth were thus to be attributed to the carbon dioxide gas added in equal amounts and in the same manner to all pots receiving gas treatments.

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[5] NOYES, H. A., The effect on plant growth of saturating a soil with carbon dioxide. Science N.S. **40**: 1914.

Equal weights of thoroughly mixed soil were put in paraffined Wagner pots of the most approved type (fig. 1). The soil in all pots was compacted by dropping each pot on the cement floor an equal number of times. Distilled water was added through the tubes to bring the moisture content up to one-half saturation, where it was kept by successive additions of water throughout the periods of investigation. The relative position of the pots was changed at regular intervals to correct differences in exposure and temperature in the greenhouse.

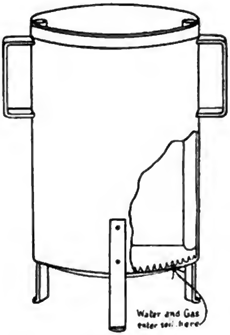

Fig. 1.—Wagner pot showing subirrigation tubes in place.

Experiment A

The Christmas pepper (*Capsicum annuum abbreviatum*) was the first plant used. Plants were started in November 1915 in the greenhouse from seed, and transplanted February 1 into the Wagner pots. The soil used was Sioux silt loam. The plants were about 1.5 inches high and carbon dioxide treatments were commenced after the plants became established. Three pots containing 4 plants each received no applications of carbon dioxide, 3 others received carbon dioxide applications 8 hours each day, and yet another set of 3 pots received carbon dioxide applications constantly. The gas was applied at the rate of approximately 650 cc. per hour, and fig. 2 shows the method of getting the gas from the pipe line to the individual pot. The wash bottles served as a means of equalizing the flow of gas into each pot. Fig. 2 shows the Christmas pepper plants after 4 months' treatment. At first the carbon dioxide treatment retarded growth, but by the time the picture was taken there was no great difference in size between the treated and untreated plants. Fig. 3

shows representative roots where no carbon dioxide gas was applied. The roots were uniformly long and fibrous and extended to the bottoms of the culture pots. Representative roots grown where the carbon dioxide treatment was 8 hours per day are shown in fig. 4. These roots did not penetrate to a depth lower than 7 inches. They were clumped and coarser when compared with those to which no carbon dioxide treatment was given. Aërial roots were quite prominent, and the main root was very thickly set with branching roots at a depth of about 3 inches. The roots shown in fig. 5 are representative of those that grew when the carbon dioxide treatment was constant. They compare unfavorably with those obtained under no treatment and under intermittent treatment. Aërial roots are many and prominent. The main roots are dwarfed and coarse and irregular. No roots were found at a depth lower than 5 inches. The carbon dioxide gas added to soil growing the Christmas pepper caused abnormal root developments. The gas had a much greater effect on the root development of the pepper plant than was apparent in the aërial portions.

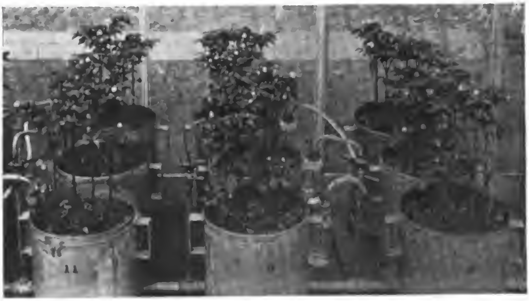

FIG. 2.—*Capsicum annuum abbreviatum* 4 months after carbon dioxide gas treatments were started: row of pots fronted by no. 11 received constant carbon dioxide treatment; row fronted by no. 8 received 8 hours' carbon dioxide treatment daily; row fronted by no. 3 received no carbon dioxide treatment.

The soil used for experiments B, C, and D was a fine sand, which has been classified by the Bureau of Soils as Wabash sandy loam. This soil was chosen because of its excellent physical condition and low organic matter content.

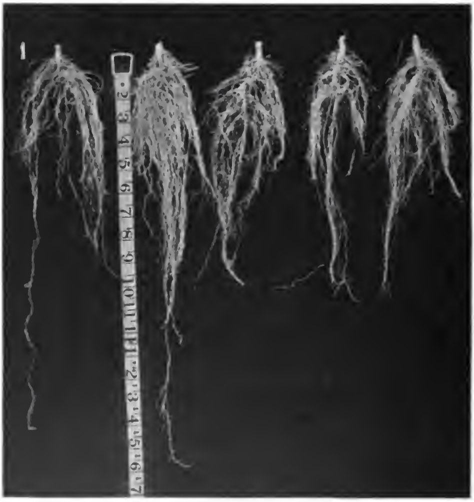

FIG. 3.—Representative roots of Christmas pepper plants which received no carbon dioxide gas treatments.

Experiment B

Head lettuce plants (*Lactuca sativa*) about 2.5 inches in diameter were transplanted into the pots in March 1917. Carbon dioxide treatments were started at once. Fig. 6 shows the best of each of the 3 triplicates. It is noted that carbon dioxide gas appears to have benefited the plants receiving treatment. These plants retained their relative sizes until harvested about 3 weeks later.

Fig. 7 shows the roots from the 2 most representative of each set of 3 plants grown under the different treatments. Carbon dioxide has affected the roots of these plants, although not to the extent that it did those of the Christmas peppers. Root development departs from normal with increased carbon dioxide applications.

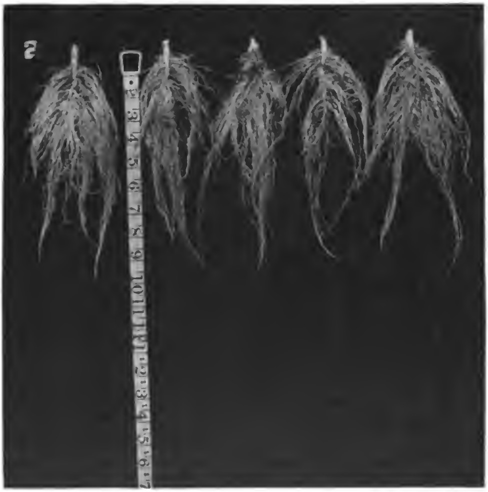

FIG. 4.—Representative roots of Christmas pepper plants which received 8 hours' treatment of carbon dioxide daily.

Experiment C

Radishes (*Raphanus sativus*) of the variety "Rapid Red" were sown in Wagner pots in March 1917. None of the plants were disturbed after the seed was sown. At the time of harvest the series of plants receiving no carbon dioxide gas applications had straight tap roots, while the roots of those receiving the gas showed a perceptible tendency to horizontal growth. Large numbers of small roots were growing from the base of the bulbs in approximately horizontal directions. No photographs were taken of this experiment.

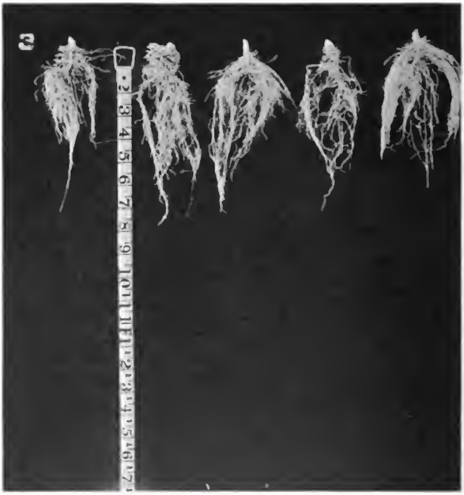

FIG. 5.—Representative roots of Christmas pepper plants which received constant treatment of carbon dioxide.

Experiment D

Burpee's stringless green pod bean (*Phaseolus vulgaris*) was grown from seed without and with the 2 carbon dioxide gas treatments. The plants were harvested just after blossoming ceased. Fig. 8 shows the plants growing in the best of each set of triplicate pots. The difference between the plants growing in the 3 pots is small. Fig. 9 shows the roots of the plants appearing in fig. 8.

Carbon dioxide gas additions to the soil did not prevent the roots from penetrating deeply, for in all pots the roots penetrated to the bottom. It was noted that roots grew to very near the openings where the carbon dioxide gas entered the pots. The gas had an effect on the development of the roots of the bean plant that was different from that observed with any other plant tested. The

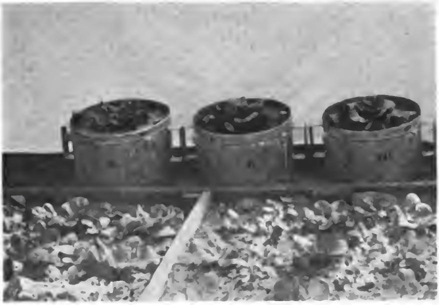

FIG. 6.—Best 3 *Lactuca sativa* of 9 under comparison: pot at left received no carbon dioxide, one in middle 8 hours daily, one at right constant treatment of carbon dioxide.

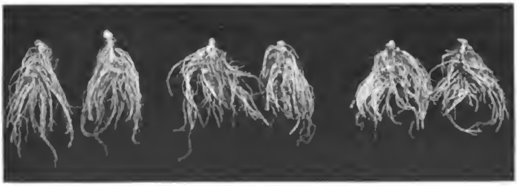

FIG. 7.—Representative roots of *Lactuca sativa:* 2 at left no carbon dioxide treatments, 2 in middle 8 hours' carbon dioxide treatment daily, 2 at right constant treatment with carbon dioxide.

intermittent carbon dioxide treatment was apparently about optimum for the development of the roots of this plant.

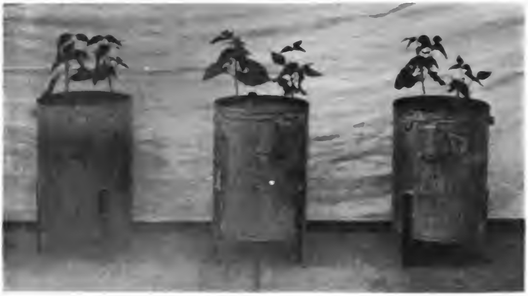

FIG. 8.—*Phaseolus vulgaris* subjected to different carbon dioxide treatments: pot at left received no carbon dioxide treatment, one in middle received 8 hours' treatment daily, one at right constant carbon dioxide treatment.

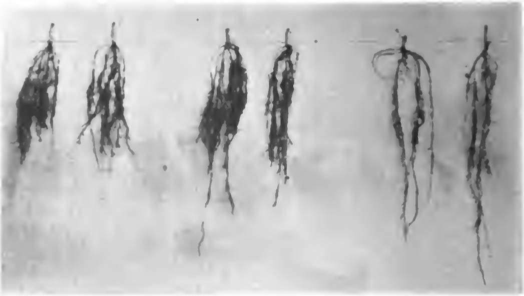

FIG. 9.—Roots of plants shown in fig. 8: 2 at left no carbon dioxide treatments, 2 in middle 8 hours' carbon dioxide treatment daily, and 2 at right constant carbon dioxide treatment.

Summary

1. Plants respond differently to carbon dioxide gas added to the soil in which they are grown.

2. The roots of the Christmas pepper, head lettuce, radish, and string bean were all found to be affected by additions of carbon dioxide gas to the soil.

3. The effects of carbon dioxide on root development were greater than those on the aërial portions of the plants.

4. The intermittent and constant applications of the carbon dioxide gas did not affect the roots of all the plants to the same extent.

5. The effect of the gas was not the same for the different plants used, although a constant treatment of 650 cc. of carbon dioxide gas per hour was apparently preventative of normal root development.

6. Decaying organic matter is held to be beneficial to growing plants. Cases have been cited by others where turning under immense amounts of green material has hurt the land temporarily; therefore the results obtained in these experiments lead to the belief that the carbon dioxide content of garden soils is sometimes detrimental to the root development of some plants growing in the garden.

7. The conclusion of CANNON and FREE that soil aëration must be a factor of no less importance in plant growth than water and temperature is supported.

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ABSORPTION OF SODIUM AND CALCIUM BY WHEAT SEEDLINGS[1]

HOWARD S. REED

(WITH ONE FIGURE)

Sea water, mammalian blood, and certain artificial solutions in which living cells are immersed are capable of continuing the life of those cells for considerable periods of time. These so-called "balanced solutions" may contain different ions which, separately, have a marked deleterious effect upon the cell, but which, when present in certain proportions, "balance" or "antagonize" each other. The result is that organisms live normally in such solutions.

There are two ways in which the mixture of ions or molecules in a balanced solution may overcome cytolytic factors: (1) by "antagonizing" each other, that is, by opposing and mutually excluding each other at the surface of the plasmatic bodies or other units of living structure; (2) by producing in the organism such a state of "tolerance," that is, by producing effects on the intracellular complexes, either alone or in conjunction with each other, that the harmful effects of single ions or molecules are eliminated. Or, in other words, the antagonism of ions may be either peripheral or internal.

Until recently the majority of physiologists were inclined to the former view, a view which was clearly stated in TRAUBE's "sieve theory of permeability" and in OVERTON's "lipoid-solubility" theory. Of the many objections to these two theories and to their various modifications, none was more cogent than that based on the fact that, even in a balanced solution, ions do slowly enter the cell. Indeed, if such were not the case, it would be impossible for the cell to obtain the salts necessary for its existence.

The objections to the former ideas of "antagonism" and "tolerance" have largely been met by a theory of antagonism proposed by OSTERHOUT,[2] which holds that the slow penetration of salts may produce effects on the cell quite different from those produced by rapid penetration, and that their action is on the life processes rather than on the manner or rate of penetration. "From this point of view we regard the slow penetration of salts in balanced solutions not as the cause but as the result of antagonism, or rather we may regard the slow penetration and the increased length of life (or growth, etc.), by which we measure antagonism, as the results of certain life processes which are directly acted on by the antagonistic substances."

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[1] Paper 47, from the University of California, Graduate School of Tropical Agriculture and Citrus Experiment Station, Riverside, California.

OSTERHOUT found that the theory was satisfactorily supported when the penetration of certain known mixtures of NaCl and $CaCl_2$ into living cells was studied. He makes, however, a seeming exception in the case of solutions of lower concentration, stating: "Below the saturation point[3] the relative proportions of the salts will be of less importance than their total concentration; this is the case at low concentrations in the region of the so-called 'nutritive effects.'"

SHIVE and TOTTINGHAM, on the other hand, not to mention others, have rather definitely shown that there are certain distinctly favorable ratios in nutrient solutions of equivalent concentration.

In view of OSTERHOUT's rather sweeping exclusion of nutrient solutions of low concentration, it seemed profitable to the writer to investigate the effect of some of OSTERHOUT's proportions in weak solutions, coupled with analyses of the plants to determine the amounts of solute taken up. It is a pleasure to acknowledge my indebtedness to Mr. J. F. BREAZEALE for the cultures and analyses upon which this work is based.

The experiments to be reported were conducted on wheat seedlings grown on disks of perforated aluminum buoyed by glass bulbs in such a way that the aluminum disk floated at the surface of the solution. Each disk was floated on about 3 liters of solution in an agate enameled pan. The seeds were germinated in a solution of the same composition as that designed for the experiment. None but sprouted seeds were used. Each disk originally held about 1000 seedlings, but careful selection brought the number down to about 200.

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[2] OSTERHOUT, W. J. V., The penetration of balanced solutions and the theory of antagonism. Science, N.S. **44**:395. 1916.

———, A dynamical theory of antagonism. Proc. Amer. Phil. Soc. **55**:533. 1916.

[3] The term "saturation point" as used is taken to mean the point at which the surface of a plasmatic structure is saturated with the antagonizing salts. Beyond this point an increase in their concentration in the solution produces no effect on their concentration in the surface.

In attempting to study the effect of a small amount of calcium, special precautions are necessary, owing to the abundance of calcium compounds in our environment. The seeds and apparatus used must be washed in dilute HCl and rinsed with distilled water of undoubted purity. The cultures must be carefully protected from dust, especially dust from plastered walls, or from cement floors, which might carry salts of calcium, since 1 part per million of calcium may produce distinct effects. It is necessary to work in somewhat the same way as one works with cultures of bacteria.

The antagonism of calcium and sodium has been a matter of record in connection with OSTERHOUT'S data. The case is illustrated by the cultures shown in fig. 1, which show the toxic action of 4000 p.p.m. NaCl and the antidoting action of $CaSO_4$, CaO, and $Mg(HCO_3)_2$. The wheat seedlings shown in the figure were similar at the outset and grew 7 days in the respective cultures. The concentration of 4000 p.p.m. NaCl is about the toxic limit for wheat seedlings under these conditions, yet 30 p.p.m. of a calcium salt antagonized completely the toxicity. Magnesium bicarbonate was not so successful in overcoming the bad effects of sodium chloride.

A further illustration of the antagonistic action of calcium is shown in table I, which gives data pertaining to wheat plants grown in solutions of sodium chloride with and without the addition of CaO. It will be seen that (1) measured by ash content and by dry weight of plants the addition of 30 p.p.m. CaO was beneficial to growth; (2) the amount of NaCl absorbed by the plants was not decreased when CaO was added. In the case of cultures 4 and 5 of table I the ratio of NaCl to total ash is 1:1.9 where only NaCl was present in the solution and 1:2.3 where both NaCl and CaO were present. From this it would seem that the calcium salt has not benefited the plant by excluding sodium, especially in view of the amount found in the tops, but rather has rendered it harmless within the plant.

A second set of cultures was made in which the ratios of sodium to calcium were identical with some of those employed by OSTERHOUT. The pure NaCl and $CaCl_2$ solutions were each 0.004M. This is much less than the concentration of NaCl employed in the first series, being 230 p.p.m. of NaCl instead of 4000 p.p.m. This series of cultures was continued for 16 days, at which time 100 representative plants were withdrawn from each culture, weighed, and analyzed, giving the data shown in table II.

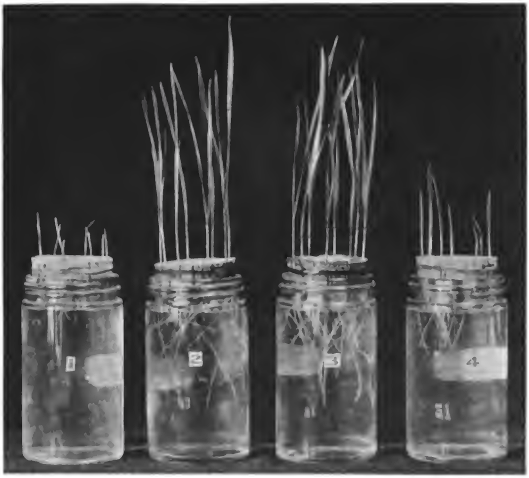

FIG. 1.—Effect of calcium and magnesium salts upon toxicity of sodium chloride to wheat plants: culture solutions were jar 1, 4000 p.p.m. NaCl; jar 2, 4000 p.p.m. NaCl plus 30 p.p.m. $CaSO_4$; jar 3, 4000 p.p.m. NaCl plus 30 p.p.m. CaO; jar 4, 4000 p.p.m. NaCl plus 30 p.p.m. $Mg(HCO_3)_2$.

It seems quite evident from these results that one of the ratios of Na:Ca in which OSTERHOUT found the greatest amount of antagonism was the one most favorable for growth in this series.

TABLE I

EFFECT OF CALCIUM OXIDE ON GROWTH AND ABSORPTION OF SODIUM CHLORIDE BY WHEAT PLANTS

Plants grown in	Days	Analysis of 100 tops		Analysis of 100 entire plants				
		Ash	NaCl	Green weight	Dry weight	Ash	CaO	NaCl
1. Distilled water	8	0.0462	trace	......	2.077	......	......	trace
2. 4000 p.p.m. NaCl	8	0.0775	0.0320	......	1.993	......	......	0.0553
3. Same plus 30 p.p.m. CaO	8	0.0921	0.0334	......	2.352	......	......	0.0595
4. 4000 p.p.m. NaCl	10	......	......	7.6	1.740	0.0940	0.0006	0.0485
5. Same plus 30 p.p.m. CaO	10	......	......	12.2	1.820	0.1240	0.0030	0.0543
6. Distilled water	8	......	......	......	......	0.0570	0.0026	......
7. 4000 p.p.m. NaCl	8	......	......	......	......	0.0660	0.0009	......
8. Same plus 30 p.p.m. CaO	8	......	......	......	......	0.0910	0.0017	......

Plants grown in the solution containing 98Na:2Ca attained the greatest dry weight and were larger than any others in the series. From this solution the greatest amount of ash constituents was absorbed and also the greatest amount of sodium. None of the other solutions appeared to contain as favorable a ratio of sodium to calcium, although the dry weight of plants in the last 4 solutions does not vary enough to offset the experimental error. The

TABLE II

WHEAT PLANTS GROWN 16 DAYS IN SOLUTION CULTURES; 100 PLANTS WITH SEEDS ATTACHED

Ratio of Na and Ca in solution	Composition of 100 plants				Ratio of Na to ash
	Dry weight	Ash	Ca	Na	
1. 100Na: 0Ca	2.10	0.1950	0.006	0.017	1:11.5
2. 98Na: 2Ca	2.74	0.2250	0.0102	0.022	1:10.2
3. 85Na: 15Ca	2.37	0.1730	0.0106	0.019	1:9.1
4. 65Na: 35Ca	2.41	0.1842	0.0132	0.016	1:11.5
5. 38Na: 62Ca	2.27	0.1930	0.0204	0.012	1:16.1
6. 0Na: 100Ca	2.33	0.2040	0.0226	0.008	1:25.5

Na:ash ratio in the first 4 sets of plants does not show any real difference. In the last 2 the relative amounts of sodium are less.

The amounts of sodium and calcium actually absorbed and retained by the plants may be of more interest to consider because they will show what the plants in the various cultures actually "fixed." The results shown in table III are taken from table II,

TABLE III

AMOUNTS OF NA AND CA ABSORBED FROM SOLUTIONS BY WHEAT PLANTS IN 16 DAYS

RATIOS FURNISHED	AMOUNTS ABSORBED	
	Na	Ca
1. 100Na: 0Ca	0.009	0.000
2. 98Na: 2Ca	0.014	0.0042
3. 85Na: 15Ca	0.011	0.0046
4. 65Na: 35Ca	0.008	0.0072
5. 38Na: 62Ca	0.004	0.0144
6. 0Na: 100Ca	0.000	0.0166

and show the amounts of sodium and calcium after deducting what was found in plants grown in solutions containing none of the element in question.

These results show that the greatest amount of sodium was absorbed from the solution containing the ratio 98Na:2Ca. Less sodium was absorbed from any other combination, even from pure sodium chloride. At the same time they also show no such selective absorption in the case of calcium. The amounts of calcium absorbed increase steadily as the amount in the solution increases, reaching their maximum in pure calcium chloride. There appears to be a "preferred ratio" of calcium for sodium, but none of sodium for calcium, although more cultures employing smaller amounts of sodium chloride should have been tried.

Summary

The antagonism of calcium and sodium which has been found by other workers exists also in more dilute solutions and may be shown by chemical analyses of the plants grown therein.

Concentrations of sodium chloride which were strongly toxic to wheat seedlings were antidoted by 30 parts per million of calcium oxide.

The most successful antagonism in the concentrations employed was found when the Na:Ca ratio was 98:2. At this ratio the calcium was not found to exclude sodium from the plant, but to render it harmless after entrance. The antagonism appears to be internal rather than peripheral.

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BRIEFER ARTICLES

METHOD OF REPLACING PARAFFIN SOLVENT WITH PARAFFIN

Some years ago LAND[1] proposed a method of insuring the gradual saturation with paraffin of the xylol now almost universally used as the clearing medium and paraffin solvent in the paraffin method. He suggested the placing of a section of fine wire screening below the level of the xylol in the shell vial upon which the paraffin ordinarily grated into the vial would be held. Such an arrangement obviates the danger of allowing the paraffin fragments to fall to the bottom of the container, there to be in contact with the material and to surround it almost at once with a high percentage of dissolved paraffin.

For some years previous to the publication of LAND's suggestion in this matter we had been employing, in this laboratory, similar devices to insure the gradual saturation of the paraffin solvent. Some time ago, however, we replaced this method for most material with another which is more simple and has given consistently good results. In this scheme melted paraffin is carefully poured on the surface of the xylol in a shell vial until a plug of the desired thickness is formed. A hot needle run around the inside of the vial will loosen the plug of paraffin, which is then pushed down below the level of the xylol. We have never found an instance in which the paraffin plug slipped down to the bottom of the vial or indeed changed its original position appreciably.

The entire paraffin plug becomes rather rapidly saturated with xylol and a layer of xylol-paraffin soon forms at the lower surface of contact. If the vial is not shaken, a very gradual saturation of the xylol takes place, and at the end of 4–6 days the xylol has taken up its maximum quantity of paraffin. In practice we pour a plug of paraffin which will weigh 4–6 gr. into a vial containing 10–15 cc. of xylol.

The increase in time required according to this scheme in the paraffin method seems justified by the rather ideally slow replacing of the paraffin solvent by paraffin. It is often desirable to cool the vial containing the xylol under the tap before pouring in the paraffin. The latter step requires only slight practice to be successful, and indeed the only effect of a too rapid pouring in of the melted paraffin seems to be the formation of strings of paraffin reaching down into the xylol. If the paraffin plug needs to be removed at any time, this can be accomplished readily by forcing through it a hot needle, the tip of which has been bent at right angles. The needle after cooling for an instant may be turned slightly and the plug pulled from the vial.—T. H. GOODSPEED, *University of California.*

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[1] LAND, W. J. G., Microchemical methods, an improved method of replacing the paraffin solvent with paraffin. BOT. GAZ. **59**: 397. 1915.

ADAPTATION AND NATURAL SELECTION

I wish to correct a false impression which my paper on the agency of fire in the propagation of the longleaf pines (BOT. GAZ. **64**:497–508. 1917) has left in the minds of some of my correspondents, to whom it seems that the conclusions there reached might lead to the absurd economic paradox that forest fires should be encouraged for the conservation of our pine lumber supply. As a matter of fact, all the evidence produced in that paper was intended to show that it is their *adaptation for resistance* to fire which insures the survival of this species. The action of natural selection in this case, as in practically all others that have come under my observation, is negative and indirect. It preserves not by selection of the fit, but by elimination of the unfit, thus giving the best adapted a free hand in the struggle for existence.

In calling attention, therefore, to the peculiar relation between the longleaf pine and fire, there was no thought of suggesting that we should imitate the method of nature; but having learned that a clean forest floor and plenty of sunshine are essential conditions for the propagation of the longleaf pine, these conditions may be secured by other means than fire, such as judicious cutting and thinning, and a periodic cleaning up of the forest floor. Whether a well guarded ground fire at the proper season might not be a useful aid in accomplishing this last purpose is a question which must be left for the practical forester to decide.—E. F. ANDREWS, *Rome, Ga.*

CURRENT LITERATURE

MINOR NOTICES

Mosses and ferns.—A third edition of Campbell's well known textbook[1] has appeared. The body of the text is the same as in the second edition of 1905, the new material being added in the form of an appendix, under the corresponding chapter headings. In addition to numerous contributions by other investigators, the appendix contains noteworthy results of the author in his investigations of tropical liverworts and ferns. The bibliography is completely recast, including 772 titles, distributed among 336 authors. The author has rendered an important service to morphologists in bringing up to date, and in convenient form, our knowledge of these great groups.—J. M. C.

NOTES FOR STUDENTS

Mitochondria.—Guilliermond has published a number of short reports dealing with the results of his investigations on the nature and function of mitochondria. In a paper[2] dealing with the origin of chromoplasts and pigments, he finds that chromoplasts are formed from mitochondria, more especially from the elongated forms called chondriocontes; and that pigments of the xanthophyll and carotin groups are elaborated either (1) directly by the mitochondria, or (2) by chromoplasts which arose from mitochondria, or (3) by chromoplasts resulting from a metamorphosis of chloroplasts which in turn arose from mitochondria. Added interest is given because of the fact that in a great many plants the process can be observed in the living material under the microscope. Both granular and crystalline pigments have the same origin. Epidermal cells from petals of *Iris germanica*, *Tulipa suaveolens*, *Tropaeolum majus*, and young fruits of *Arum maculatum*, *Asparagus officinalis*, and numerous others furnished the material for this study.

In a later paper[3] dealing with the chondrium of *Tulipa*, he reports that the mitochondria are easily visible in the living material under the oil immersion lens. Epidermal cells from petals are used. The mitochondria are long, thin, and undulate, although smaller granular and rod mitochondria are present. Material is at its best just about the time the flowers first open. The reviewer has verified these observations with the yellow-flowered variety, but was not successful with the white ones, and found further that the mitochondria begin to disintegrate in the course of 30 minutes after the mount is made.

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[1] Campbell, D. H., The structure and development of mosses and ferns (Archegoniatae). 3d ed. 8vo. pp. 708. *figs. 322*. New York: Macmillan Co. 1918. $4.50.

[2] Guilliermond, A., Compt. Rend. Acad. Sci. **164**:232–235. 1917.

[3] ———, *Loc. cit.* **164**:407–409. 1917.

In a third paper[4] dealing with alterations of the chondrium, he finds that "the mitochondria are the most fragile elements of the cell, and it is through them that the first signs of degeneration and the first symptoms of trouble due to osmotic changes are manifested." The alteration consists of the transformation of the mitochondria into vesicles having the aspect of vacuoles and giving the cytoplasm an alveolar appearance. This, the author remarks, is interesting when we think of BÜTSCHLI's alveolar structures.

In a fourth paper[5] dealing with the fixation of cytoplasm, he finds that from the point of view of their action on the chondrium fixing agents may be grouped in three classes: (1) alcohol, Mann's, Zenker's, and Carnoy's fluids all disturb the structure of the cytoplasm and destroy the mitochondria; (2) picric acid, mercuric chloride, formalin, and strong Flemming's generally cause a pronounced shriveling of the mitochondria, often accompanied by a diminution of the chromaticity of these structures; (3) Altmann's, Benda's, Regaud's, and Flemming's with only a trace of acetic acid are the fixing agents commonly used for fixing mitochondria and the cytoplasm as nearly like living as possible. In general it is those reagents which contain alcohol or acetic acid which alter the mitochondria most.

MOTTIER[6] has published a valuable contribution to the study of mitochondria, not only in the new facts he has revealed, but more especially in the account of his methods, which will enable workers much less qualified to take up studies in this interesting field. In the main he used Flemming's fluid, with very much reduced amounts of acetic acid for a fixative and iron haematoxylin and crystal violet for stains. For material he used root tips of *Pisum sativum*, *Zea Mays*, and *Adiantum pedatum;* the thallus of *Marchantia polymorpha*, *Anthoceros*, and *Pallavacinia;* seedlings of *Pinus Banksiana;* leaves of *Elodea canadensis;* and certain algae.

He finds that root tips of *Pisum* furnish excellent material for a study of the primordia of plastids and their transformations. Mitochondria-like structures are very numerous, such as rods of various lengths and thicknesses, straight, variously curved and bent, and also numerous smaller granules and slender delicate rods. Leucoplasts develop from the larger structures, but the smaller ones do not form plastids. Although these structures all give the same histochemical reactions, the term chondriosome (mitochondrium) is reserved for those smaller structures which do not form plastids. The former he calls "plastid primordia." *Zea Mays* is similar in all essentials to *Pisum.* In *Marchantia* the "plastid primordia" are more readily distinguished from the mitochondria in that they are larger and rounded, while the mitochondria are very small granular or rod forms. Cells from the thallus of *Anthoceros* were studied because they have each a single chloroplast and hence furnish favorable objects for determining whether mitochondria are merely disorganized chloroplasts. This question is answered in the negative. In *Adiantum pedatum* he finds that the mitochondria are small, granular, and rod-shaped. Discussion is here confined to root tips, and we are promised a subsequent paper dealing with other parts. The "plastid primordia" are rounded, lenticular, and rod-shaped, but much larger than the mitochondria. The rod-shaped "primordia" which do not develop into leucoplasts "continue to elongate into long-drawn-out threads and finally disappear." In the younger growing parts of the stem of *Pinus Banksiana* numerous small rounded bodies with colorless centers (plastid primordia) and densely staining granules (mitochondria) were found. In the older parts these bodies with the colorless centers form the plastids, while the granular mitochondria have become larger or formed rod mitochondria. In the leaves of *Elodea canadensis* the primordia are rod-shaped and can easily be traced in their transformation into plastids. The mitochondria are very numerous, and in cells with fully developed chloroplasts they are globular and even rod-shaped, differing from the primordia only in size. We are promised a later paper dealing with his results on *Hydrodictyon*.

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[4] GUILLERMOND, A., *Loc. cit.* **164**:609–612. 1917.

[5] ———, *Loc. cit.* **164**:643–646. 1917.

[6] MOTTIER, D. A., Chondriosomes and the primordia of chloroplasts and leucoplasts. Ann. Botany **32**:91–114. *pl. 1.* 1918.

Guilliermond includes under the term mitochondria all those structures which give the same histochemical reactions, regardless of their functions; while Mottier, on the other hand, considers only those structures which do not develop into plastids to be included under the term. Both, however, agree that these structures are "morphological units of the cell with the same rank as the nucleus." Mottier goes farther and asks, "What characteristics are transmitted solely by the nucleus, and what by the primordia of plastids and by the chondriosomes? There are many transmissible characteristics which cannot as yet be definitely expressed in any Mendelian ratio. To claim that certain phenomena of fluctuating variations and other numerous characteristics, Mendelian or otherwise, owe their appearance and transmission to the primordia of plastids and chondriosomes may be a daring hypothesis, but if, as there is good ground to believe, these bodies are permanent organs, there is no escape from some such assumption."—Ray C. Friesner.

Units of vegetation and their classification.—With the advance of the science of ecology there has been a gradual evolution of opinion as to the units most suitable for the analysis and study of vegetation. The earlier stages of this evolution have been well discussed by Moss,[7] who also advanced the developmental concept of the plant formation. The half decade following this paper passed without a further notable contribution to the subject, but recently three articles have appeared that are notable, not only for the divergence of the views expressed, but also for the decided advance they have made in providing a logical system of classified units for the use of students of vegetation.

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[7] Moss, C. E., The fundamental units of vegetation. New Phytol. **9**:18–53. 1910.

GLEASON[8] embodies in his article an individualistic concept of ecology, contending that all phenomena of vegetation depend upon the phenomena of the individual plant. The plant association he conceives to be an area of uniform vegetation developed by similar environmental selection from the immigrants from the surrounding population. This position, while extreme, will prove most useful if it serves to focus attention upon the intensive study of some of the most important species of a vegetation so as to discover their reactions to various environments and to the factors which limit their invasion and establishment in plant communities.

The other extreme is seen in the work of CLEMENTS,[9] as expressed in what doubtless is the most notable of recent contributions to ecological literature. Without attempting to review or criticize his book as a whole, it may be pointed out that he selects the formation as the fundamental unit and regards this plant community as an organic entity exhibiting origin, growth, maturity, and death. As an organism it is able to reproduce itself and possesses a life history which is a complex but definite process. The climax community is the adult organism of which all initial and medial stages are but stages of development. Thus CLEMENTS would limit the term formation to the climax community, while the successional series leading up to the climax formation he calls a "sere." He has provided a complete system of subordinate units for the analysis of both formation and the sere, the former being divided successively into associations, consociations, societies, and clans; the latter into associes, consocies, socies, colonies, and families. This recognition of a plant community as an entity comparable in some extent at least to an organism seems strictly in accord with the views of most ecological workers, and if the relationship be regarded as one of close analogy rather than homology it will probably prove the most stimulating and satisfactory attitude. It appears, however, that CLEMENTS' system of subordinate units is rather more elaborate than is required to meet the needs of most investigators.

A somewhat simpler system, introducing but few new concepts or terms, recently organized by NICHOLS,[10] commends itself to the reviewer as including those units and terms which in the past have proved most satisfactory, and which now for the first time have been combined in a definite system. NICHOLS himself claims that the scheme is the outgrowth of the classification originally presented by COWLES,[11] and by his selection of the association as the fundamental unit of vegetation he recognizes the tendency of ecologists as a whole to become more and more agreed upon the use of the term "plant association," even while differing somewhat as to the content of the term. He defines the association as any community of plants, taken in its entirety, which occupies a common habitat, or in other terms, any stage in a given successional series. The "habitat," thus made the criterion of the association, is understood to be a unit area with an essentially uniform environment made up of a complex of climatic, edaphic, and biotic factors which determine the ecological aspect of the vegetation. The subdivisions of the association agree with those of CLEMENTS in being consociation and society, but differ in that "association" (and its subdivisions) is applied to both the climax and the seral units.

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[8] GLEASON, H. A., The structure and development of the plant association. Bull. Torr. Bot. Club **44**:463-481. 1917.

[9] CLEMENTS, F. E., Plant succession. Carn. Inst. Wash. Pub. 242. pp. xiii+511. *pls. 61*. 1916.

[10] NICHOLS, GEO. E., The interpretation and application of certain terms and concepts in the ecological classification of plant communities. Plant World **20**:305-319, 341-353. 1917.

Here NICHOLS has added a most useful although rather abstract concept of "association type," defined as "a type of plant association which is correlated with a given type of habitat." The association type which represents the highest degree of mesophytism which the climate of the region permits is regarded as the regional climax. It has been usual to regard as permanent only such associations as are included in such a regional climax type, but NICHOLS holds that in edaphically unfavorable situations not only is succession much slowed down, but that it often becomes permanently arrested at a point far short of the climax just mentioned. In this way there would be developed permanent associations less mesophytic than the regional climax association type. These may be distinguished as belonging to an "edaphic climax." Most ecologists recognizing this situation have preferred to regard such associations as belonging to a "temporary climax," postulating the eventual although much delayed dominance of a climax limited by climate only.

Grouping plant associations upon a developmental basis, the plant community of the next higher order is termed an "edaphic formation" and defined as "an association-complex which is related to a specific physiographic unit area." Here the "formation" differs from that of CLEMENTS in including not only the climax community but also those of seral rank. Edaphic formations are in turn grouped into "edaphic formation-types" and the "edaphic formation-complex" for any climatic region constitutes a "climatic formation." In this use of the terms edaphic formation and climatic formation NICHOLS has retained the well known classification of SCHIMPER, while modifying the concepts to include the developmental idea. The various climatic formations belong to various "climatic formation-types," several of which may form the "climatic formation-complex" of a continent or other large unit area.

NICHOLS has further demonstrated the utility of his excellent scheme of classification by applying it to the analysis of the vegetation of northern Cape

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[11] COWLES, H. C., The physiographic ecology of Chicago and vicinity. BOT. GAZ. 31:73–108, 145–235. 1901.

Breton Island, appending various explanatory remarks which should prove useful to students attempting to make similar applications to other regions.—GEO. D. FULLER.

Permeability.—Several interesting contributions to our knowledge of protoplasmic permeability have appeared recently. DELF[12] has investigated the influence of temperature on the permeability of protoplasm to water by the tissue shrinkage method, using sections of onion leaves and dandelion scapes in subtonic solutions of cane sugar. The curve of contraction at different temperatures was measured by means of an optical lever which greatly magnified the shrinkage, and from this curve the rate of contraction at the time when 30, 50, and 70 per cent of the shrinkage had occurred, was measured by the tangents to the curves at these points. From the rates the values for Q_{10} were obtained. This value increases as the temperature rises. In the onion leaf the value of Q^{10} at 10–20° C. is 1.5, at 20–30° C. is 2.6, and at 30–40° C. is 3.0. In the dandelion scape the greatest value of Q_{10} was obtained at 20–30° C., at which temperatures it was 3.8. Above and below those temperatures the value falls. Contrary to the results of VAN RYSSELBERGHE, who found very little increase in permeability above 20° C., DELF finds that permeability of the protoplasm to water continues to increase rapidly up to the highest temperature investigated, 42° C. The methods used by VAN RYSSELBERGHE are justly criticized, particularly with reference to the means of deriving a temperature relation from his data. The strength of solutions used by VAN RYSSELBERGHE may also have led to serious errors.

Miss HIND[13] has studied the absorption of acids by living plant tissues, using electrical conductivity methods, and electrometrical measurement of the H^+ ion concentration in acid solutions which were in contact with living potato disks and roots of *Vicia Faba*. She found that the hydrogen ion is rapidly absorbed from dilute acid solutions by living tissues, and concluded that the anion, particularly in organic acids, plays a large part in determining the effects of the acid on protoplasm. In the case of the mineral acids, HCl, HNO_3, and H_2SO_4, the stronger solutions can penetrate the cells for a time without causing much injury as measured by exudation of electrolytes; but organic acids like formic and acetic cause very rapid increase in conductivity, due to exosmosis of electrolytes from the cell. With these two acids there is first a decrease and then after a few hours a very noticeable increase in H^+ ion concentration. This is thought to be due possibly to the production of acids within the tissues which diffuse out through the altered plasmatic membrane.

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[12] DELF, E. MARION, Studies of protoplasmic permeability by measurement of rate of shrinkage of turgid tissues. I. The influence of temperature on the permeability of protoplasm to water. Ann. Botany **30**:283–310. 1916.

[13] HIND, MILDRED, Studies in permeability. III. The absorption of acids by plant tissue. Ann. Botany **30**:223–238. 1916.

As to the mechanism of absorption, a few experiments furnish evidence favoring the idea that the plasmatic proteins rather than the lipoids are active in the acid absorption.

A very important paper by **STILES** and **JØRGENSEN**[14] challenges not only the theory of permeability proposed by **CZAPEK** some years ago, the surface tension theory, but also all the facts and assumptions upon which that theory was founded. Because of its greater exactness and more general applicability to a study of all kinds of plant tissue, the Kohlrausch electrical conductivity method of estimating osmosis of electrolytes was used as a means of measuring changed permeability. Disks of potato were placed in non-electrolytic reagents of such strength as to produce irreversible changes in the protoplasm. Exosmosis of electrolytes was measured in the presence of a number of homologous monohydric alcohols, chloroform, chloral hydrate, ether, urethane, acetone, aniline, and pyridine. In all cases corrections for the depression of conductivity caused by the presence of the non-electrolyte in the external solution were made. In every case the rate of exosmosis was found to depend upon the concentration of the substance in solution in contact with the disks. The higher the concentration the more rapid the exosmosis, and **CZAPEK**'s observation that any member of the homologous series of primary alcohols has a greater effect on osmosis than a lower member of the series, if of equimolecular concentration, is confirmed. No such thing as a critical concentration, however, below which exosmosis did not occur and above which it did occur, could be found. Exosmose of electrolytes occurred in all concentrations used, down to mere fractions of the critical concentrations for exosmosis found by **CZAPEK**'s crude methods. The rate of diffusion of electrolytes was found not to be a function of surface tension alone. If the critical concentration of isobutyl alcohol were to be taken as 0.3 M. and the other alcohols compared with it as to equal exosmosis in a given time, the surface tensions of the various alcohols do not agree at 0.68 of the surface tension of water, as **CZAPEK** stated, but vary from 0.79 in methyl alcohol to 0.59 in isoamyl. The higher the alcohol the greater the lowering of the surface tension required to produce a given amount of exosmosis in a given time. Each item of evidence and the whole tissue of assumptions upon which **CZAPEK** built his theory of the plasmatic membrane is considered in detailed fashion and without gloves. The authors reject each point and assumption as untenable. In their own words, "from this review of the details of Czapek's work on the plasma membrane, it is clear that neither the experimental evidence nor any part of the theory based upon it can be accepted." They have sought to apply the law of mass action to the rate of osmosis in cases of permeability involving irreversible changes in the protoplasm, and a mathematical expression has been deduced connecting the time element with exosmosis. Curves representing the equation derived thus on theoretical grounds resemble in type those obtained in actual experiments. The methods used in this work seem admirably adapted to a crucial test of CZAPEK'S theory, which seems entirely untenable in view of the evidence submitted.—CHARLES A. SHULL.

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[14] STILES, WALTER, and JØRGENSEN, INGVAR, Studies in permeability. IV. The action of various organic substances on the permeability of the plant cell, and its bearing on CZAPEK's theory of the plasma membrane. Ann. Botany **31**:47–76. 1917.

Desiccation.—An investigation of the course of desiccation and partial starvation in cacti has been made by MACDOUGAL, LONG, and BROWN.[15] The principal studies center upon the changing rate of water loss, chemical changes in the food reserves, plasmatic colloids, and cell sap, and the morphological changes which occur during long periods of desiccation. In one case a large *Echinocactus* was under observation for 6 years after removal of the plant from the soil. Water loss is rather rapid at first, but proceeds more and more slowly with time. While 10 per cent of the water was lost the first year in one specimen, during the sixth year only 5 per cent of the water remaining at the beginning of that year was lost. The loss of water is much more rapid of course in the open than in diffuse light and *Echinocactus* can withstand desiccation not more than 2 years with free exposure.

The chief chemical changes noted during the starving period concern the carbohydrates. The density of the cell sap decreases, due to disintegration of the carbohydrates, and the reducing sugars are found mainly in the inner part of the cortex in desiccated specimens rather than near the surface as in normal plants. The total amount of reducing sugars decreases during desiccation, while non-reducing sugars are increased noticeably in the cell sap. Reduction of the amount of sugars leads to reduction of acidity if the light intensity is sufficient for photolysis of the acid. In weak light even, if the sugars run low, the acids may accumulate because of the absence of photolysis. Differences in acidity are thought to be partially responsible for differences in the colloid hydration and swelling of tissues when placed in water.

The main morphological changes consist in thickening of the cuticle, thinning of the anterior walls of the guard cells, partial destruction of the plasmatic colloids, shrinkage in the size of the nucleus, and especially the development of cortical lacunae through hydrolysis of the cell walls of this region of the stem. The vascular tissues are not affected, and the medullary cells much less than the cortical cells.—CHARLES A. SHULL.

The vegetation of Michigan.—From the data obtained during a few weeks in Michigan, HARPER[16] has listed the principal plants in the order of their abundance and has discussed certain features of the environment. He recognizes but two types of succession, the one from the filling up of lakes and other depressions, and the other that following fire. In connection with the former, he distinguishes the usually recognized types of marsh and bog vegetation and states that the main distinction between the two is in the rate of growth, the slow rate of growth in bog plants being largely explained upon the basis of a dearth of mineral plant food in the substratum, which is also supposed to account for the presence of the same species upon the uplands in colder climates. No experimental evidence is given in support of this explanation. It is also rather surprising to be told that bog vegetation is "sometimes erroneously called xerophytic," after the almost endless discussion of bog xerophytes.

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[15] MACDOUGAL, D. T., LONG, E. R., and BROWN, J. G., End results of desiccation and respiration in succulent plants. Physiol. Res. 1:289–325. 1915.

[16] HARPER, R. M., The plant population of northern lower Michigan and its environment. Bull. Torr. Bot. Club 45:23–42. 1918.

A deficiency of mineral plant food is also given as an explanation of the slow progress toward mesophytism of the pine forests upon sandy uplands. Leaching is supposed to prevent the accumulation of any considerable amount of plant food near the surface of the ground. This may possibly hold for the sandy plains, but if so it is difficult to see why it should not also apply to the pure sand of the dunes, where mesophytic forests develop rather quickly and where the conifers are soon largely replaced by deciduous species.

In discussing the influence of fire upon forest establishment, the error is made of stating that the cones of *Pinus Banksiana* remain closed and attached to the tree for many years, opening and discharging their seed after burning. Closer observation would have shown that the cones that remain for several years upon this pine open and discharge their seed very promptly upon ripening, and that the tree is in no wise dependent upon fire for its seeding.—GEO. D. FULLER.

Fairy rings and their effect on vegetation.—Of more than ordinary interest is a recent paper on fairy rings by SHANTZ and PIEMEISEL.[17] Before taking up their own researches, they present an excellent summary of past studies and theories concerning them, as well as a table of the fungi that have been reported as being responsible for rings. Some fungi, as *Agaricus tabularis*, are very destructive to grass and other vegetation; some, as *Calvatia* and *Lycoperdon*, are beneficial; and some, as *Lepiota*, have little effect of any sort. Striking conclusions are given relative to the age of rings. The conditions in eastern Colorado are not very favorable, either for spore germination or mycelial advance; in favorable years there may be a mycelial advance from the ring center of 30–60 cm., as compared with almost no advance at all in dry years. Some of the rings are very large, and from the growth measurements that have been made, a few are estimated to be 400–600 years old. Where vegetation is stimulated, it was concluded from careful study that this is due to the reduction of nitrogenous organic matter to available nitrates and ammonia salts, and to the subsequent decay of the fungous filaments. Deterioration or death of vegetation are attributed mainly to drought, caused by the prevention of water penetration by the masses of fungal filaments. Vegetation thus destroyed is replaced, after the death of the fungous, first by weeds, then by short-lived grasses, and eventually by the original short-grass cover.—H. C. COWLES.

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[17] SHANTZ, H. L., and PIEMEISEL, R. L., Fungous fairy rings in eastern Colorado and their effect on vegetation. Jour. Agric. Research 11:191–246. *pls. 21. figs. 15.* 1917.

Foreign pollen on Cycas.—It is well known that in some cycads the ovules reach the maximum size for the species whether pollination has occurred or not; while in others the ovules, if not pollinated, soon disorganize. *Cycas Rumphii* belongs to the latter category.[18] Female plants of this species are very abundant in Ceylon, but no male plants have been observed for several years. In localities where male cones of *Encephalartos* and *Macrozamia* are abundant, the pollen of these species germinates in the pollen chamber of *Cycas Rumphii* and causes the ovule to develop to the full size. Since the pollen of cycads germinates readily in artificial solutions, it is not strange that pollen of one species should germinate in the pollen chamber of another. In this case, however, no fertilization takes place, and mature seeds, which should show the embryo in an advanced stage of development, showed no trace of an embryo. A few years ago the reviewer pollinated *Stangeria* with *Zamia* and obtained three large seeds, which were planted but failed to germinate. It is possible that the pollen stimulated growth but failed to fertilize the egg, so that, as in *Cycas Rumphii*, no embryo was produced.—CHARLES J. CHAMBERLAIN.

Water culture.—In a critical discussion of the water culture method of studying growth phenomena, STILES[19] calls attention to the limitations of the method. He points out the great complexity of the factors involved, and applies BLACKMAN'S idea of limiting factors. The difficulty of analyzing the results of such experiments, due to the interaction of so large a complex of factors, few of which, even those whose action is under investigation, can be controlled, is made clear. Some factors, as for instance the influence of the respiratory activity of the roots on the culture solutions, have been neglected in all water culture work. The variability of individual plants is so great that a large amount of labor is required to secure results even with a low degree of accuracy. Nevertheless, for certain kinds of problems it may be the only method available.—CHARLES A. SHULL.

Grasses of Illinois.—Miss MOSHER[20] has published a manual of the grasses of Illinois, recognizing 204 species in 63 genera, over one-fifth of the species being recorded for the first time as occurring in Illinois. The analytical keys, descriptions, and numerous text cuts make the bulletin very useful in the recognition of the grass flora.—J. M. C.

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[18] LE GOC, M. J., Effect of foreign pollination on *Cycas Rumphii*. Ann. Roy. Bot. Gard. Peradeniya **6**:187–194. *pl. 13*. 1917.

[19] STILES, WALTER, On the interpretation of the results of water culture experiments. Ann. Botany **30**:427–426. 1916.

[20] MOSHER, EDNA, The grasses of Illinois. Univ. Ill. Agric. Exper. Sta. Bull. 205. pp. 261–425. *figs. 287*. 1918.

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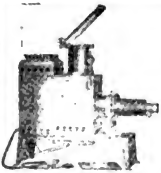

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THE

BOTANICAL GAZETTE

NOVEMBER 1918

MORPHOLOGY OF RUMEX CRISPUS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 244

WINFIELD DUDGEON

(WITH PLATES XVII–XIX AND TWENTY-ONE FIGURES)

Introduction

A chance examination of a stem of *Rumex crispus* L. showed the presence of well developed internal bundles. Since this character is to be regarded as advanced, Dr. W. J. G. LAND suggested that it might be of interest to investigate the morphology of the entire plant. This paper is concerned only with an account of the morphology of the floral structures; a study of the vascular situation is already under way.

Aside from monographs, the genus *Rumex*, and indeed the entire family Polygonaceae and order Polygonales, have received little attention. FINK (3) made a study of the ovular structures in *R. verticillatus* L. and *R. mexicanus* Meisn. (*R. salicifolius* Man.), which develop very similarly. The archesporial cell cuts off a primary wall cell, then forms a linear tetrad, the innermost megaspore of which functions. He found approximately 24 chromosomes in the spindle of the first division of the megaspore mother cell, but was not certain whether this was a true reduction division. A regular 8-nucleate embryo sac is formed, and pollen tubes enter, although actual fusion of the gametes was observed but once, and that in an unfavorable preparation. ROTH (8) investigated several European species of *Rumex*, among them *R. crispus*. He found the haploid number of chromosomes in the microspore mother cells to be 8 in *R. Acetosa*, *R. hispanica*, *R. arifolius*, and *R. nivalis;* 16 in *R. Acetosella;* and probably 40 in *R. cordifolius*. *R. Acetosa* apparently undergoes reduction in the megaspore mother cell, although he saw no indication of subsequent fertilization. The embryo sac very frequently degenerates. He found evidence of apogamy in some species, and thinks it probable that, at least in the group *Acetosa*, this has been the result of dioecism. STRASBURGER (**9**) early investigated *Polygonum divaricatum*, and his figures of the origin and development of the embryo sac have become a classic example of normal behavior.

Material and methods

Inflorescences and individual flowers of various ages were collected along street borders near the University of Chicago, and in a flood plain pasture near Mineral Springs, Indiana, during the summers of 1915 and 1916. They were killed in chrom-acetic, imbedded in paraffin, and cut in the usual manner. Both iron alum-hematoxylin and safranin-gentian violet were employed for staining.

Some of the most important features of the morphology became apparent in the course of the investigation during the winter of 1916–17, and as no more material could be obtained then, there remain some points the solution of which requires the collection of more flowers and careful observations on the growing plants.

Normal development

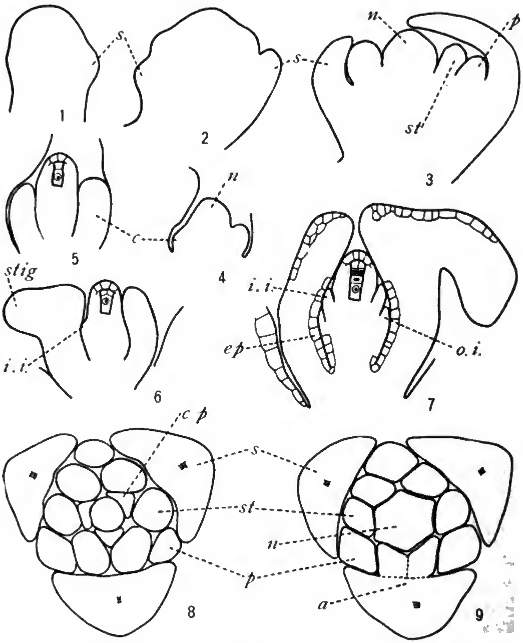
ORGANOGENY.—The young inflorescence of *Rumex crispus* is closely invested by the sheaths of successive bracts. It is profusely branched, and the branches bear flower buds of considerable size before they emerge from the protecting sheaths. All the young parts are covered with a mucilaginous secretion, rendering the penetration of reagents slow.

The flowers are borne in clusters at the nodes. The oldest are nearest the main stem, while the successively younger arise outside these, on the upper surface of the enlarged projecting nodes.

The sequence of development of the floral organs is centripetal, although the petals and carpels are somewhat delayed (figs. 1–7). The sepals appear as 3 thick prominences, and rapidly grow up over the young flower. The 3 petals appear almost simultaneously with the stamens, which they closely resemble at first (figs. 3, 8, 9). The 6 stamens appear in pairs, the 2 of each pair arising so close together that their bases are joined to each other and to the sepal opposite which they lie (fig. 9*a*). The carpels first appear as a thick ring about the base of the nucellus, but the latter develops much more rapidly and is not inclosed by them until the megaspore mother cell is considerably enlarged (figs. 4–7). The carpels develop as a continuous ring led by 3 growing points (fig. 8), until the ovarial cavity is inclosed, when the 3 points continue separately to form the styles and stigmas (figs. 6, 7). The styles are reflexed so that the much branched stigmas are finally placed between the bases of the anthers.

The inner integument appears during the prophase of the first reduction division (fig. 6), and the outer appears with the homoiotypic division (fig. 7). Both are 2-layered from the beginning. The inner grows up beyond the nucellus, and turns inward to close up and form the micropyle. The outer integument never extends much beyond the tip of the nucellus. During the development of the embryo sac, the cells of the outer layer of the outer integument and the epidermis of the ovary thicken, lose their contents, and form a continuous impervious layer (fig. 7; see also figs. 13, 14). This process is significant, because it leaves only the chalazal region of the ovule as a point of intake for nutrient materials.

MEGASPOROGENESIS.—The terminal cell of a definite axial row in the nucellus enlarges as the archespore (fig. 22). It soon divides to form the primary parietal cell and the megaspore mother cell (fig. 23). The parietal cell divides twice by anticlinal walls to form a cap of 4 cells (figs. 24, 28). Occasionally any or all of these cells may divide by a periclinal wall (figs. 25, 32). Less frequently, a cell or two of the adjacent epidermis may also divide periclinally (figs. 33, 36, 44). Occasionally there are two archesporial cells, and in one ovule there was a mass of probably 7 archesporial cells, a few of which had undergone the first division. In the most



FIGS. 1–9.—Organogeny: fig. 1, appearance of sepals (*s*); figs. 2, 3, simultaneous appearance of petals (*p*) and stamens (*st*), nucellus (*n*); figs. 4, 5, early development of carpels (*c*); fig. 6, appearance of inner integument (*ii*) and beginning of stigma (*stig*); fig. 7, appearance of outer integument (*oi*) and early thickening of epidermal cells (*ep*) over outside of ovule and walls of ovary; figs. 8, 9, transverse sections of same flower, showing relation of parts, growing points of carpels (*cp*), and union of stamens to each other and to sepal (*a*); figs. 1–7, ×175; figs. 8, 9, ×155.

advanced case observed, the 2 megaspore mother cells had fully enlarged and were in prophase of the heterotypic mitosis (fig. 24). They were separated by a crushed cell of equal length, which may have been a megaspore mother cell, but more probably was only a vegetative cell that became so crushed that it could not divide, and was forced to elongate with the enlarging mother cells.

The megaspore mother cell enlarges and elongates considerably, then undergoes two successive divisions to form a tetrad of cells (fig. 28). Apparently this division is a true reduction, for all the stages seem to be normal, and at diakinesis there are 32 pairs of chromosomes (fig. 26). While an accurate count of the chromosomes could not be made on the spindle, careful estimation indicates that the number still is 32 (fig. 27). In the vegetative cells the spindle is shorter, and proportionally much broader, and while the chromosomes are too small and too densely massed to be definitely counted at any stage, they clearly are more numerous than in the megaspore mother cell; I could only estimate that there are about twice as many, that is, 64.

Wall formation follows each of the reduction mitoses. The first wall usually divides the mother cell a little above the center (fig. 30). The second wall is usually near the outer end of the inner cell (figs. 29, 30), although in the best preparation found (fig. 28) the cell is nearly equally divided. The wall in the outer cell is always longitudinal, instead of transverse (fig. 28). There is some irregularity in the sequence of the homoiotypic division; usually the inner cell divides first (fig. 30); sometimes the divisions are simultaneous (fig. 28); and in one case the outer cell was the first to divide.

The inner megaspore functions, and the others quickly degenerate (fig. 29). The third megaspore rarely forms a normal cell, and is usually the first to degenerate (figs. 31, 33). The outer cell may degenerate before it has a chance to divide, or the 2 megaspores may degenerate before they are separated by a wall (fig. 31).

EMBRYO SAC.—The functioning megaspore rapidly elongates and develops a large vacuole at each end, with the nucleus centrally placed (figs. 33–35). The daughter nuclei migrate to the poles, where two more mitoses produce 8 nuclei (figs. 38, 42, 44). The mature sac is of the usual organization (fig. 46). The outer end enlarges greatly, crushing the parietal and adjacent nucellar cells, and comes to lie in contact with the epidermis of the nucellus. The extreme inner end remains small through this and subsequent development, and in it the 3 antipodal cells are cut off by walls. While they persist until the embryo is of considerable size, they never manifest any activity (fig. 47). The polar nuclei fuse early (figs. 44–47), and the fusion nucleus lies well toward the outer end of the sac. The egg apparatus is typical.

DEVELOPMENT OF STAMENS.—The stamen primordia are at first oval in cross-section (fig. 8), but early differentiation of the archesporial cells makes them somewhat rectangular, and sets off the anther region from the filament. The archespores are single rows of cells (fig. 48); each soon divides by a periclinal wall to form the primary parietal cell and the primary microsporogenous cell (fig. 49), then both divide anticlinally. Frequently the anticlinal division precedes the periclinal (fig. 50). There are 2 periclinal divisions in the primary parietal cell, and an appropriate number of transverse divisions to keep pace with the rapidly elongating anther. The first (fig. 54) sets off a layer that finally differentiates into a well marked endothecium with characteristic spiral thickenings; the second (fig. 57) forms the middle wall layer and the tapetum, and takes place about the same time as the last division in the sporogenous tissue. The middle layer is soon crushed and obliterated (fig. 58).

The tapetal cells appear to behave in all possible ways. According to BONNETT (1) the nucleus usually divides twice by normal mitoses, after which there may occur a great variety of nuclear fusions and abnormal mitoses. In some cases there is but one division. Usually in *Rumex crispus* the tapetum becomes binucleate; often it is multinucleate; and now and then there may appear large irregular nuclei with many nucleoli, as if formed by the fusion of a number of small nuclei (fig. 61). Apparently the normal condition is for the tapetum to persist as a functioning nutritive layer up to the liberation of the microspores from the tetrad (fig. 63); but in keeping with the widespread degenerations occurring throughout the flower, it may begin to degenerate while the microspore mother cells are entering reduction (fig. 58). The cytoplasm becomes vacuolate, the nucleus stains very deeply, and shortly the entire protoplast collapses.

Before the microspore mother cell stage, the epidermis over most of the anther begins to enlarge and thicken, and the protoplasts to disorganize. This thickening extends to the cells of the connective, so that each loculus becomes inclosed by an impervious layer, except in the stomial region (fig. 10). Here a plate of the epidermis a few cells wide, together with the outer half of the tissue between adjacent loculi, remains undifferentiated, as a special mechanism for dehiscence. As the anther matures, these weak cells break down, first joining the cavities of the adjoining loculi to form the pollen chamber, then opening this chamber to the exterior.

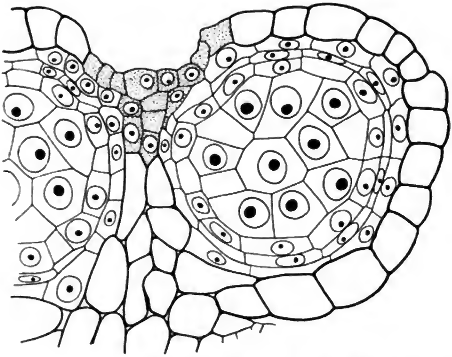


FIG. 10.—Portion of transverse section of fully differentiated anther, showing thickened epidermis continuous with thickened connective, and permanently juvenile tissue (shaded), subsequent disorganization of which first connects the two adjacent loculi, then dehisces the resulting pollen chamber; ×730.

MICROSPOROGENESIS.—The primary sporogenous cells undergo three or four successive divisions to form the completed sporogenous tissue. At the same time the anther has elongated greatly, so that in each loculus there come to be 9–12 mother cells in transverse section, and 15–20 in longitudinal section (fig. 57). Just before reduction there is conspicuous enlargement of the anther, stretching the walls of the mother cells, and allowing the protoplasts to round off. The cytoplasm of the mother cells is rather dense and finely granular, and the nuclei are large with scanty chromatin.

Reduction appears to be normal. No attempt was made to trace the details. At diakinesis there are 32 pairs of chromosomes (fig. 60), as found in the megaspore mother cells. The formation of a tetrahedral tetrad, the development of a thick cellulose wall about it, wall formation about the microspores, and liberation of the microspores from the tetrad by disorganization of the thick common wall, all follow the usual procedure for dicotyledons. At first rather dense, the cytoplasm of the microspores does not keep pace with the enlargement of the cell, and becomes rather finely vacuolate (fig. 64)., It is not certain whether this is entirely normal; indeed, degeneration is so universal that it is difficult to determine whether there is such a thing as normal development of the microspore.

The nucleus of the microspore divides into tube and generative nuclei, and the latter organizes a small cell about itself (figs. 67, 68). Before shedding, the generative cell produces two male nuclei (figs. 71, 72); very few pollen grains ever reach this stage with anything approaching what may be considered normal appearance. The exine becomes well thickened and delicately rugose. Three germ pores are formed, beneath which the intine is slightly thickened (figs. 65, 66); they are connected with each other by furrows over the surface.

FERTILIZATION.—Any conclusion for or against fertilization must for the present depend entirely on negative evidence. Some of the facts observed point rather conclusively to the occurrence of fertilization. There is no doubt that there is diakinesis in the megaspore mother cell, that there are 32 diads, and that this is the number present in the microspore mother cells also. While the exact number of chromosomes on the spindle of the heterotypic mitosis could not be counted, it appears to be 32 (fig. 27); the achromatic figure has all the characteristics of a reduction spindle; and finally a tetrad of cells results. Further, the polar nuclei fuse early, a process characteristic of normal haploid embryo sacs; and a fair number of embryos is formed. Many embryo sacs have the appearance of having waited a long time for fertilization, before finally degenerating (fig. 47). On the other hand, there is equally convincing evidence that fertilization does not occur. I cannot be sure that I have seen normal pollen in any instance; that which might be considered normal is so scarce that there seems little chance for adequate pollination. Some pollen grains have been observed on the stigmas, but they all had the appearance that is believed to indicate degeneration, and certainly none of them was germinating. At the same time, the stigmas wither early, and most of them would seem to be incapable of supporting pollen tube growth. No pollen tubes were ever observed, either in the styles or in the micropyles, nor any densely staining remains that might indicate the position of former tubes. The dead impervious layer over the outer integument would seem to preclude the entrance of pollen tubes through any other point than the micropyle and the tip of the nucellus. No fusion of gametes, which after all is the final proof of fertilization, was seen; indeed, in all the preparations I have made and examined I have seen just one embryo sac that contained a normal appearing egg apparatus (fig. 46), and it was in a still unopened flower. In the many flowers I have examined in section, only a relatively small number contained embryos.

It is possible that *Rumex crispus* behaves as OVERTON (7) found for *Thalictrum purpurascens*, where some megaspore mother cells undergo normal reduction, producing haploid embryo sacs and reduced eggs that require fertilization for further development, while other megaspore mother cells fail to reduce, and give rise to diploid sacs and eggs, the latter developing embryos apogamously. If this should prove to be the situation in *Rumex crispus*, then it would be expected that the embryos arise apogamously from unreduced eggs. I regret that there has been no opportunity to collect new material to settle this important question.

SUBSEQUENT DEVELOPMENT OF FLOWER.—It is beside the purpose of this paper to discuss the details of fruit development, and only the early stages have been investigated. As previously mentioned, only a relatively small number of flowers ever proceed to fruit formation. The embryo and endosperm are of the well known *Capsella* type; the suspensor may become about 10 cells long, and occasionally some of the cells divide longitudinally. All parts of the ovule elongate greatly, and the integuments and walls of the nucellus finally become compacted into a single thin layer. The carpels become much thickened and the cells strongly lignified. The petals enlarge and elongate to keep pace with the developing fruit, and function as protective organs (valves), while the tissue on the abaxial side of the midrib of each proliferates and forms the characteristic tubercles. The sepals alone, of all the structures in the maturing flower, fail to enlarge, and remain tiny flaps at the bases of the petals.

Degenerations

It soon became apparent that the most striking and significant feature in the flowers of *Rumex crispus* is the wholesale degenerations that occur. These degenerations may go on in either the stamens or the carpels, or in both at the same time. They are characterized in some cases by lighter staining and increasing vacuolation of the cytoplasm, until it becomes an almost indistinguishably thin peripheral layer, and the aggregation of the chromatin into fewer and larger masses, with irregular outline of and final collapse and disintegration of the nucleus. Such changes are characteristic in the earlier stages of development of the stamens. In other cases, the cytoplasm increases in density and staining power, and plasmolyzes away from the walls; the nucleus becomes deeply and uniformly granular, and finally stains as a solid homogeneous mass; the protoplast ultimately shrinks into a blob in which no trace of the original structure can be distinguished.

DEGENERATIONS IN THE STAMENS.—Degenerations in the stamens may begin at any stage, from the primary sporogenous cell to the pollen grain, and may involve part or all of the sporogenous tissue, part or all of the microspore mother cells, one to all of the spores of a tetrad, any or all of the microspores, and any or all of the pollen grains, in any or all of the loculi of the anthers, in any or all of the flowers of an inflorescence, and may or may not be accompanied by disorganization of the corresponding parts of the anthers. No instance has been observed of failure of all 6 anthers to start normal development, and nothing indicating disturbances in this development appears in the archesporial cell stage. It is very common, however, for the primary sporogenous cells to acquire small vacuoles (fig. 50), which merge into larger and larger vacuoles (fig. 51), until finally the cytoplasm is only a thin membrane lining the walls of the cell. It stains less and less intensely as the process goes on. The chromatin becomes aggregated into fewer and larger masses, which lie closely appressed to the nuclear membrane, and which stain very deeply. The nucleolus soon becomes indistinguishable. The nucleus becomes irregular in outline and shrinks, and in turn almost disappears. At the same time, the primary parietal cell, connective cells, and surrounding epidermis undergo a similar disorganization. Such a process usually is not confined to a single loculus, or even to a single anther, but includes all the stamens of a flower. Apparently if the degeneration process is not intense such cells may continue dividing for a time, forming anthers with all parts in normal relation (figs. 55, 56). Finally the cells become too weakened to divide further, and are nearly or quite empty. Anthers may be found in this condition that have developed almost to the mother cell stage. In the end, the arrested stamens break down and disappear completely before the flower opens.

In other flowers the anthers may start normally, but individual cells in the sporogenous mass begin to degenerate, while the others, at least for a time, appear to continue normally (figs. 53, 54). Both cytoplasm and nucleus become more coarsely granular and very dense, and stain intensely. The protoplast pulls away from the cell walls, finally becoming only a shapeless dense mass in the central part of the cell. This process involves all the loculi of all the anthers of a flower, and may occur at any stage up to and including the mother cells.

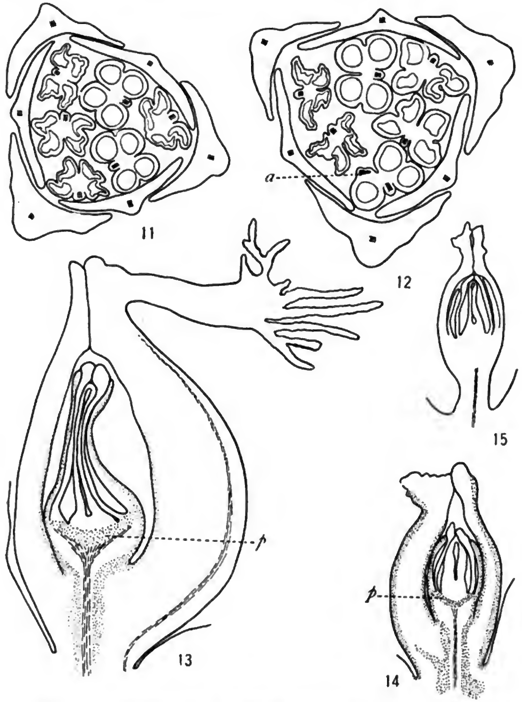
Normal microspore mother cells round off evenly and uniformly when the anther enlarges, and stain moderately. Mother cells in the process of degeneration round off into irregular masses, and stain more or less intensely according to the degree of disorganization. These cells are capable of passing through the reduction divisions (fig. 61), and chromosome number, spindles, and the tetrads formed appear to be normal in essential features, but they stain very deeply and the outlines are irregular.

Usually if the anther walls have developed unimpaired to the reduction stage, they can reach maturity and produce a normal appearing organ. Many, however, begin to collapse, and it is very common to find examples in which the walls have collapsed closely against the sporogenous tissue within, while the cells and walls are much wrinkled and distorted (fig. 61). Earlier degenerations are likely to include all the stamens of a flower; later degenerations may include only one or two loculi of one anther, or only one or a few of the 6 anthers (figs. 11, 12). In one case in particular, one of the loculi of an anther had degenerated early and left only a small deeply staining spot at the side of an otherwise normal organ (fig. 12*a*).

As already mentioned, the tapetum is involved along with the other parts. A few anthers have been observed in which the sporogenous cells had degenerated completely into dense shapeless masses, while the walls and tapetum had remained relatively unaffected; the wall cells were thicker than normal, and the tapetal cells had become much larger and projected like papillae against the contracted, disorganized, sporogenous tissue (fig. 59).

By the time reduction is completed, the tendency to degeneration has become so universal that only a few microspores appear normal. It is not uncommon to find even the spores of a tetrad in widely different stages of disorganization; one or two will appear almost normal, while the others are mere masses of stain (fig. 62). In such cases it is certain that spores that do not stain so intensely are really affected. Spores that survive liberation from the tetrad may shrivel up, with the cytoplasm more and more closely packed about the diminishing nucleus, until finally nothing is left but the wall with a little mass collapsed against one side (figs. 63, 65, 66).

Very many spores proceed to wall formation and the usual divisions to complete the male gametophyte. Only in a few



FIGS. 11–15.—Various degrees of degeneration in flower: figs. 11, 12, transverse sections of flowers at tetrad stage of microspores, showing indiscriminate failure of anthers; at *a*, fig. 12, a loculus disorganized early, while other three are developing normally; fig. 13, ovary well developed, ovule just beginning to collapse, and embryo sac with small amount of completely disorganized endosperm; fig. 14, both embryo sac and ovule disorganized; fig. 15, ovary in which degeneration began so early that nothing remains but dried remnants; shaded parts in figs. 13, 14 indicate thickened impervious cells, particularly chalazal plate (*p*); ending of ovular vascular bundle also shown; figs. 11, 12, ×50; figs. 13–15, ×155.

instances, however, do the cells produced look as if they might be normal. The cytoplasm is much vacuolated, and the nuclei are not distinct, even in the best of preparations (figs. 67, 68, 72, 73).

HYPERTROPHY OF POLLEN GRAIN.—Those grains that appear most nearly normal have little or no starch (fig. 67). Pollen grains that have proceeded to full wall development and generative cell formation begin to enlarge until about twice normal volume (fig. 68). In all such there is considerable accumulation of starch grains, and in some the cell is tightly packed with relatively enormous grains (fig. 69). Whenever the nuclei show at all, they are irregular in outline, poorly defined, and almost uniform in texture. Later, the starch is dissolved, and the contents of the pollen grain become more and more homogeneous, until in the end the grain is filled with a granular substance staining deeply and uniformly throughout. In the best preparations, some of these cells still showed the remains of the nuclei; but there is little doubt that they are destined to go to pieces (figs. 70–73). In every case the tube nucleus was irregular and difficult to trace, but often the two male nuclei, although very small, still held their shape and showed separate chromatin masses. Usually, however, only deeply and characteristically staining masses indicate the remains of the nuclei (figs. 71, 72, 75).

"POLLEN TUBE" FORMATION.—Hypertrophy of the pollen grains may be due to high osmotic pressure set up in the disintegrating contents. The starch formation undoubtedly is pathological. The conditions in the cell that induce starch formation probably also cause other changes, which lead to greatly increased osmotic pressure, which is further increased by the solution of the starch. Very frequently these large pollen grains put out pollen tubes through all three of the germ pores. These tubes may remain mere bulbs (fig. 72), or they may become many times the length of the cell producing them, and are always almost solidly filled with the dense homogeneous contents of the mother cell (figs. 74, 75). Often the disorganizing nuclei migrate into the tubes, and the pollen grain may be almost entirely emptied (fig. 74). The tubes often become inflated at the end, as if under pressure, and it appears that they sometimes burst.

The explanation of these tubes seems to be that the high osmotic pressure set up in the pollen grain literally blows the distensible intine out through the germ pores, and continues elongation of the tube as long as the pressure is maintained. Presently the pressure goes down and the process ceases. It may be that the retention of some semblance of organization by the nuclei indicates that the cell is not dead, and that tube formation is a weak abnormal growth process. Finally, the contents of the grain begin to shrivel (fig. 74), the walls become wrinkled and collapse, and the cell dries up. By the time the anthers open, little or no trace of the pollen tubes remains, and the nuclear material is no longer distinguishable. I would estimate that 99 per cent of the pollen grains undergo some such degeneration process. Very infrequently one can find a grain of normal size with the nuclei clearly outlined, lying among the hypertrophied grains, and occasionally one or two of the loculi of an anther will contain seemingly normal grains, while the remaining loculi are filled with the large cytolyzed grains.

FUNGUS INVASIONS.—Such a mass of disorganizing cells would seem to be particularly favorable material for the growth of saprophytes. In every dehisced anther sectioned there was an abundant growth of an unidentified fungus. The septate hyphae ramify everywhere through the pollen chambers among the pollen grains, and in a very few instances were seen penetrating pollen grains through the germ pores (fig. 70), but with the appearance of a chance entrance, rather than a definite exploitation of the contents of the grains. It may be stated confidently that the fungus does not attack unopened anthers, for it never was present until after the anthers had opened. In those anthers where the fungus had been developing longest and had formed a felt of hyphae, it had produced a great abundance of minute spores.

DEGENERATIONS IN OVARY.—Degenerations just as widespread and devastating occur in the ovary also. They do not begin so early as in the anthers, never having been observed with certainty before reduction is completed (figs. 31, 32), although there are faint suggestions that even during the second reduction division the cells may not be entirely healthy. The non-functioning megaspores seem to degenerate prematurely, although this is by no means an unusual feature in angiosperms. With the beginning of enlargement of the functioning megaspore the degeneration process becomes apparent (figs. 31, 32). It is always characterized by increasing density of both cytoplasm and nucleus, plasmolysis of the cytoplasm, and final collapse into a distorted strand in the center of the cell (figs. 36, 37). The disturbance occurs with increasing frequency through the various stages of embryo sac formation, 2- (figs. 39, 40, 41), 4- (fig. 43), and 8-nucleate (fig. 45) stages being found in more or less advanced degeneration, until by the time the sac should be mature, scarcely one remains untouched. In all the sections made and examined, I have seen just one normal appearing embryo sac. It is not a case of having overlooked the stage, for repeatedly late buds and open flowers showed the remains of sacs in all stages of disorganization (fig. 47).

At first, and in early embryo sac stages, only the sac itself is involved, but later the entire ovule becomes shriveled, with the individual cells deeply staining. If the process has begun early enough, it involves the entire ovary also. An open flower, therefore, may show all parts of the ovary normal except the embryo sac (fig. 13), or both embryo sac and ovule may be degenerating (fig. 14), or the entire ovary may be shriveled up, brown, and dead, a mere husk projecting up from the base of the flower (fig. 15).

Degenerations do not halt here, but may attack those ovaries in which embryo formation has begun. At any stage in the development of the fruit the ovule may collapse about the embryo and endosperm, which then take on the characteristic dense, deeply staining appearance. The ovary itself appears sometimes to continue normal development, at least for a time, or it may follow the other parts in degeneration. Certainly not more than 10 per cent of the flowers examined in section contained embryos, and of these not more than 10 per cent had the appearance of being able to reach maturity in a normal manner.

It is very striking that in every case a plate of dense impervious cells, several layers thick, was formed across the chalaza, connecting at the edges with the impervious layer over the outer integument and the ovary walls. Other and irregular patches of similar tissue appear in the funiculus, often seeming to involve even the cells of the ovular vascular bundle (figs. 13, 14, 20). This bundle flares out against the lower side of the impervious chalazal plate (fig. 13), and there is no passage of normal cells anywhere connecting it with the nucellus. The lower end of the bundle terminates blindly in a patch of permanently thin-walled parenchyma, with absolutely no connection with the vascular system traversing the peduncle and branching to supply the other parts of the flower (figs. 19–21). Below this parenchyma, between the traces to the sepals and petals, and removed by 8–10 parenchyma cells from the end of the ovular bundle, the bundle of the peduncle terminates in a broad axial mass of short tracheids. One thinks of the patch of parenchyma as a reservoir, filled from the bottom by the bundles of the peduncle, and emptied by an ovular bundle dipping into the top.

DEGENERATIONS IN ENTIRE INFLORESCENCE.—Degenerations are not always confined to scattered flowers, but may involve all the flowers, especially the terminal portions of large or late inflorescences. The earlier in the development of the inflorescence that the degeneration processes set in, the larger is the number of flowers involved.

ABSCISSIONS.—Accompanying these degenerations is a strong tendency for parts to absciss. There is a definite abscission layer formed near the base of the peduncle (fig. 16), which leads to dropping off of those flowers in which extreme early degenerations have appeared. A ring of epidermis remains thin, and the underlying cortical cells remain meristematic. The exact method of operation has not been followed; it is probable that the mechanism is called into activity by the same causes that result in failure of the other floral parts.

The fully developed filament of the stamen is a short thick stalk, traversed by a small vascular bundle. All the mature stamens that were observed were either entirely separated from the flower, or at least physiologically separated, by disorganization of the upper end of the filaments. The epidermis and cortical cells break down, leaving the anther attached by the vascular bundle only (fig. 19*a*). Soon this is severed also, and the anther is held in the flower only by the floral envelop, to be dropped out upon blooming. The stump of the filament continues disorganizing until finally only frayed out, dried remnants remain at the point of insertion.

RESULTS OF DEGENERATIONS.—Where degenerations involve both stamens and ovary at an early age, the entire bud drops before opening. A large percentage of the flowers of an inflorescence is lost in this way. Where the degenerations involve only the stamens or only the carpels, or when beginning later in the development of the flower, 4 distinct types of mature flowers are produced, with all gradations between.

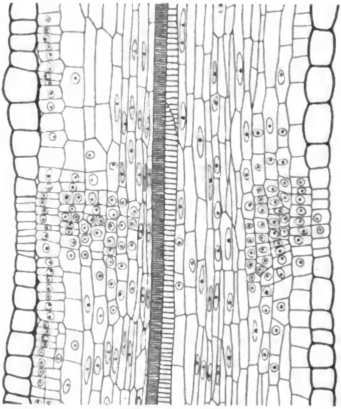
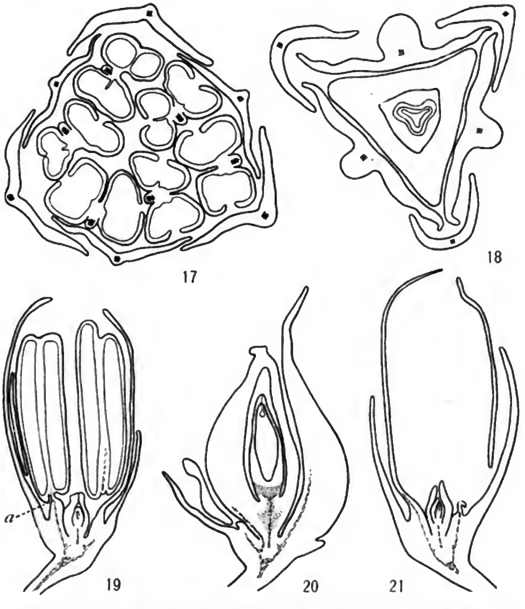


FIG. 16.—Longitudinal section through abscission region of peduncle; cells of epidermis are strongly thickened, and those of cortex are for the most part differentiated beyond point of further division, except in definite abscission zone, where divisions are still in progress; note large number of recently divided cells in subepidermal layer on left side; their subsequent elongation will produce the strong curvature of peduncle; ×350.

1. Functional staminate flowers, in which any number of stamens, from one to all, reach maturity, although their products

usually are not functional. The ovary usually is well developed, but the embryo sac is sterile by degeneration. The sepals and petals are about equally developed; they have performed their function in protecting the essential organs in the bud, and make no



Figs. 17–21.—Types of mature flowers: fig. 17, transverse section, and fig. 19, longitudinal section of a functional staminate flower; ovary is present but sterile by degeneration; anther on left in fig. 19 nearly severed by disorganization of filament at *a;* fig. 18, transverse section, and fig. 20, longitudinal section of functional ovulate flower at early stage of embryo development; stamens degenerated and disappeared before flower opened; fig. 21, longitudinal section of a sterile flower; stamens obliterated and ovule sterile by degenerations; figs. 17, 18, ×30; figs. 19–21, ×18.

further growth. The flowers have accomplished their purpose with the development of pollen, defective though that may be, and soon wither (figs. 17, 19).

2. Functional ovulate flowers, from which all the stamens have been eliminated by degeneration before the opening of the flower. In such flowers the stamens frequently disappear so early that the points of insertion are no longer discernible, and even the vascular traces have almost disappeared. An embryo begins to develop, and endosperm formation starts, although subsequently degeneration may overtake it, resulting either in death of the entire flower, or in development of a pseudo-parthenocarpic fruit. The sepals remain small, but the petals enlarge as protective organs and develop the characteristic tubercles (figs. 18, 20).

3. Bisporangiate flowers, containing both functional ovary and functional stamens. They are very rare; I have sectioned two such, and these had only one or two stamens each.

4. Completely sterile flowers, where degenerations have occurred in both stamens and carpels early enough to cause complete elimination of the former, but not severe enough to cause the flower to drop before blooming. The ovary may be in any condition from fully developed, with only the embryo sac defective, to a mere dried remnant (fig. 21).

Conclusions as to significance of degenerations

Such degenerations as have been described look toward the complete elimination of either the stamens collectively or the carpels. The process seems very severe, and results in a high mortality, not only of flowers, but of the developing fruits as well. It is a case of degeneration during the process of development, and is not to be confused with arrested development, such as occurs in the production of staminodia, and which looks toward reduction in the number of organs in the cycle involved.

The term dioecism has a very different meaning when applied to spermatophytes and when applied to cryptogams. In the latter it is assumed that separation of the sexes to distinct male and female gametophytes is a phenomenon based on heredity, and determined by chromatic constitution, and that the separation occurs during the reduction divisions. When the differentiation is pushed farther back, however, until the sporophytes producing the two kinds of spores are likewise differentiated, it is difficult to see how chromatic constitution can be made to explain the situation. It is to this later and secondary phase of sex segregation that the term dioecism is applied in seed plants. The view has been expressed in scattered papers that the particular species under investigation have been rendered diclinous by failure of either the stamen or the ovules to produce functional gametophytes, and that this process has been carried a step farther, to the complete suppression of the functioning stamens in some (ovulate) plants, and to the complete suppression of functioning ovaries in other (staminate) plants. This view has been occasioned by the discovery that more or less perfect essential organs may produce few or no functional sexual products.

Rumex seems a particularly favorable group for the study of this process, and it is believed that it shows convincing evidence for the origin of dicliny, and finally of dioecism, by degenerations during ontogenesis. The members of the section LAPATHUM, including *R. crispus*, are variously described in manuals as having hermaphrodite, polygamo-monoecious, polygamo-dioecious, andromonoecious, gyno-dioecious, etc., flowers, while those belonging to the ACETOSA section are described as dioecious. In *R. crispus*, at least, the appearance of the mature flowers evidently is misleading, for sections show that the apparently perfect flowers are almost invariably functionally staminate; the apparently staminate flowers are really such; while the apparently ovulate may be either functionally ovulate or completely sterile. These conditions are brought about by degeneration at various stages in oogenesis and spermatogenesis, and not by arrested development. The result, even in the seemingly perfect flowers of *R. crispus*, is physiological dicliny.

ROTH (**8**) found in species of section ACETOSA, which are usually exclusively dioecious, that sometimes hermaphrodite and even staminate flowers are produced, but that the pollen is defective in every case; others have found the same situation. All the species in section LAPATHUM that he investigated produced hermaphrodite flowers at first, and ovulate flowers almost exclusively later in the season. He found numerous instances of degenerating embryo sacs in *R. Acetosa*. I have examined a great many sections of *R. Acetosella*, and found no instance of such behavior. It would seem that degenerations in the ovary are much less frequent in the dioecious species than in the so-called hermaphrodite, and that when the ovulate plants occasionally produce stamens, all the pollen is functionless.

The conclusion is that *Rumex* formerly produced only hermaphrodite flowers, and that by degenerations in the stamens and in the carpels the condition has been attained such as is found in *R. crispus*, and the species of section LAPATHUM in general, where the inflorescence contains a mixture of physiologically staminate, physiologically ovulate, a few bisporangiate, and many completely sterile flowers. This is physiological dicliny. The process has been carried farther in some forms, resulting in segregation of the staminate and ovulate flowers to separate plants, as is now the case in the species in section ACETOSA. That these latter forms have been derived from bisporangiate or monoecious ancestors is indicated by the occasional production of stamens on "ovulate" plants. That this derivation has been due to degenerations is indicated by the sterility of the staminate structures when they are formed.

It seems clear that the stamens are more readily eliminated from the flowers than are the ovules. They start degenerating earlier in their development, and it is very common for all trace of them to be lost by the time the flower opens, while the ovules invariably persist in physiologically staminate flowers, and very frequently are defective only in the embryo sac.

It is probable that the degeneration processes favor the occurrence of apogamy. Not only does degeneration result in elimination of stamens from many flowers, but it results also in sterility of the pollen that is produced by normal anthers. Dioecism would render pollination by the small amount of pollen remaining normal a very uncertain process. Finally, it is altogether possible that when the degeneration process in the ovary is but weakly manifested, it may interfere with reduction in the megaspore mother cell, and may account for the long wait in the prophase of the heterotypic mitosis, and the subsequent completion of the division as a typic mitosis, as has been repeatedly reported for well marked apogamous plants.

The strong tendency to failure in the sexual process may also contribute to the development of highly successful methods of vegetative propagation. Nearly all the species of section LAPATHUM perennate by strong storage tap roots crowned by a short stem region, or by storage rhizomes, and all propagate very freely by detached fragments of these underground stems. *R. Acetosella* propagates by long lateral roots which produce new plants at intervals. It is a striking fact that patches of the plant are dense growths of almost exclusively staminate or ovulate plants. This is what would be expected to result from such vegetative propagation, and would be a curious segregation to result from plants produced to any great extent from seeds. All the evidence I have seen points to apogamy in *R. Acetosella;* seed production is very scanty in proportion to the number of flower buds, and a large percentage of the fruits are empty. A considerable number of seedlings scattered about in patches of ovulate plants indicates that many of the seeds are viable.

From the great number of diclinous angiosperm flowers that contain remnants of the other organs, it seems very probable that the degeneration processes here described are of widespread occurrence, and are scattered throughout the group from the lowest to the highest forms. It is planned to make a study of dicliny in the future, in the effort to substantiate or disprove this theory of the origin of dicliny as the result of degenerations.

The cause of these degenerations is not known. The few authors who have discussed the problem all agree that faulty nutrition is important, if not as the direct cause, at least in producing conditions that call the phenomenon into activity. HOFFMANN (5) supposed that the embryos of *R. Acetosella* and other dioecious plants are sexless, and that sex is determined in the early stages of the seedling by the conditions under which they germinate. GÄRTNER (4) used the evidence in the reverse order, and thought that degenerations in the stamens and ovules are "caused by the inherent tendency in the species to become dioecious." "Faulty nutrition" is so indefinite and vague, and includes such a wide range of possibilities that it can scarcely be considered as an adequate explanation. It is more probably a condition which calls into greater activity certain fundamental and at present unknown causes of degeneration that are always present in a wide range of angiosperm forms. It is barely possible that the peculiar detached vascular bundle of the ovule may be responsible for the failure of the ovule in later stages. This bundle never has been found connected with the general vascular system of the peduncle, even in those infrequent instances when the embryo and endosperm seem to be developing normally. If this should prove to be the immediate cause for later degenerations in the ovule, there still remains no hint of the cause for the failure of the ovular vascular bundle to make proper connections.

STRASBURGER (10) concluded from his study of the species of EUALCHEMILLA that sterility is the result of excessive mutation. It seems clear that sterility, partial or complete, results from degenerations, and probably such degenerations are the *only* morphological causes of sterility. It might follow then that excessive mutation is the cause of sterility, or it may be that mutating species are only more susceptible to degenerations.

JEFFREY (6) believes that sterility is the result of hybridization. Again, it is a question whether hybridity is a fundamental cause, or only produces physiological conditions that activate a more or less latent tendency to degenerations. If hybridity is the underlying cause of the degenerations that lead to sterility, and the theory that these degenerations lead to dicliny, apogamy, and the development of successful methods of vegetative propagation should prove to be correct, it would seem to follow that all hybrids are tending toward these states. Probably the evidence would not support this reasoning. It is more probable that there exists no causal relation between the hybrid state and degenerations, except as physiological conditions in hybrids favor such processes.

DORSEY (2) concludes from a study of grape hybrids that "hybridity is not necessarily a cause of sterility," and that "pollen sterility in the grape is only a step toward functional dicliny." All the scanty published evidence I have seen seems to support this conclusion.

Summary

1. Organogeny is normal, with slight delay in appearance of petals and carpels.

2. The megaspore mother cell produces a tetrad of megaspores, the innermost of which functions. The haploid chromosome number is 32.

3. The embryo sac is of the ordinary 8-nucleate type.

4. Microsporogenous tissue is formed from the primary sporogenous cell by 3–4 successive divisions, and reduction is normal. The haploid chromosome number is 32.

5. The mature pollen grain contains two male nuclei, the progeny of a definite generative cell.

6. There is good negative evidence both for and against the occurrence of fertilization. This raises the question whether some of the megaspore mother cells may not undergo reduction, while others only simulate reduction and give rise to a diploid embryo sac, the latter *only* producing embryos by the apogamous development of the egg.

7. Widespread degenerations occur: (*a*) in any or all of the anthers, at any stage from the sporogenous initial to the mature pollen grain, and may involve only the sporogenous tissue and its products, or the entire anther; (*b*) in the ovary, at any stage from the functioning megaspore to the maturing fruit, and may involve only the embryo sac, or both embryo sac and ovule, or the entire ovary; (*c*) in entire inflorescences.

8. Most pollen grains undergo cytolysis, with abundant starch formation, conspicuous enlargement, and the formation of "pollen tubes."

9. Only a small percentage of pollen grains and embryo sacs have the appearance of being functional.

10. An unidentified fungus invades the anthers after dehiscence, ramifying among but rarely penetrating the pollen grains.

11. There is a definite abscission layer near the base of the peduncle, cutting off either before or after blooming those flowers

in which both stamens and ovary are early involved in strong degenerations. There is also a degeneration of the filament cells, severing the maturing anthers.

12. Four types of mature flowers are produced by these degenerations: (*a*) physiologically staminate, although the pollen may or may not be functional (the ovary is functionless); (*b*) physiologically ovulate, the stamens having been completely eliminated by degeneration; (*c*) bisporangiate, having both stamens and ovary functional (very rare); (*d*) completely sterile, having functionless ovary, and stamens completely eliminated.

13. It is suggested that these degenerations may be of widespread occurrence, and probably are the cause of (*a*) dicliny, and finally dioecism, and (*b*) apogamy, and that (*c*) they favor the development of successful methods of vegetative propagation.

14. The cause of such degenerations is as yet unknown. It is suggested that deficient nutrition, excessive mutation, and hybridity bear no causal relation to degeneration, except as they may create physiological conditions favorable for it.

I wish to thank Dr. J. M. COULTER, Dr. C. J. CHAMBERLAIN, and Dr. W. J. G. LAND for their interest and assistance throughout the course of this investigation.

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EXPLANATION OF PLATES XVII–XIX

Figs. 22–75 were all drawn at an initial magnification of ×1460, with the exception of figs. 26 and 60, which were ×4400; all figures have been reduced one-half.

FIG. 22—Longitudinal section of young nucellus, showing archesporial cell terminating a definite axial row.

FIG. 23.—Archesporial cell divided into primary wall cell and megaspore mother cell.

FIG. 24.—Nucellus with 2 megaspore mother cells, both in prophase of heterotypic mitosis.

FIG. 25.—Megaspore mother cell in prophase of heterotypic mitosis; wall cells have divided periclinally.

FIG. 26.—Diakinesis in megaspore mother cell, showing 32 pairs of chromosomes, the haploid number; reconstructed from 3 sections.

FIG. 27.—Spindle of heterotypic mitosis in megaspore mother cell; plasmolysis may possibly indicate initial stage of degeneration.

FIG. 28.—Normal tetrad of megaspores.

FIG. 29.—Early degeneration of outer 3 megaspores of tetrad.

FIG. 30.—Inner cell has preceded outer in homoiotypic mitosis.

FIG. 31.—Early degeneration of functioning megaspore.

FIG. 32.—Degeneration of functioning megaspore at a slightly later stage.

FIG. 33.—Normal growth of functioning megaspore.

FIGS. 34, 35.—Normal functioning megaspores fully enlarged.

FIGS. 36, 37.—Degeneration of fully enlarged functioning megaspores.

FIG. 38.—Normal 2-nucleate stage of embryo sac.

FIG. 39.—Early stage in degeneration of embryo sac in 2-nucleate stage.

FIGS. 40, 41.—Same, more advanced.

FIG. 42.—Normal 4-nucleate stage of embryo sac.

FIG. 43.—Degeneration of embryo sac in 4-nucleate stage.

FIG. 44.—Normal 8-nucleate stage of embryo sac just beginning mature organization.

FIG. 45.—Degeneration of embryo sac in 8-nucleate stage.

FIG. 46.—Normal fully developed embryo sac.

FIG. 47.—Fully developed embryo sac in advanced degeneration, apparently after a long wait for fertilization.

FIG. 48.—Transverse section of portion of a young anther, showing archesporial cells.

FIG. 49.—Archesporial cell divided into primary parietal cell and primary microsporogenous cell.

FIG. 50.—Primary microsporogenous cells beginning to degenerate; anticlinal division preceded usual periclinal in archespore.

FIG. 51.—Primary microsporogenous cell in advanced degeneration.

FIG. 52.—First division in normal primary microsporogenous cell.

FIG. 53.—Degeneration restricted to a single cell (in transverse section) of early microsporogenous tissue.

FIG. 54.—Degeneration of isolated cells in later microsporogenous tissue.

FIG. 55.—Advanced degeneration of entire mass of microsporogenous cells; wall cells are also involved.

FIG. 56.—Same at a later stage of development; wall cells nearly normal.

FIG. 57.—Portion of normal anther at synapsis of microspore mother cells.

FIG. 58.—Same stage, with premature degeneration of tapetum.

FIG. 59.—Same stage, with microsporogenous tissue completely disorganized; middle wall layer and tapetum greatly enlarged.

FIG. 60.—Diakinesis stage of heterotypic mitosis in normal microspore mother cell, showing 32 pairs of chromosomes, the haploid number; reconstructed from 2 sections.

FIG. 61.—Transverse section of loculus of collapsed anther, in which degenerating sporogenous tissue has just completed reduction; tapetum shows variety of nuclear situations, and is still functional.

FIG. 62.—Tetrad of microspores in various stages of degeneration.

FIG. 63.—Probably normal disorganization of tapetum at a time when the microspores are well differentiated, although apparently beginning to degenerate.

FIG. 64.—Apparently normal microspore.

FIG. 65.—Microspore degenerating.

FIG. 66.—Microspore with walls completely differentiated, in advanced degeneration.

FIG. 67.—Apparently nearly normal pollen grain with generative cell organized.

FIG. 68.—Same, showing beginning of hypertrophy and starch accumulation.

FIG. 69.—Hypertrophied pollen grain, packed with large starch grains.

FIG. 70.—Hypertrophied pollen grain with contents beginning to disorganize, penetrated by a fungus hypha.

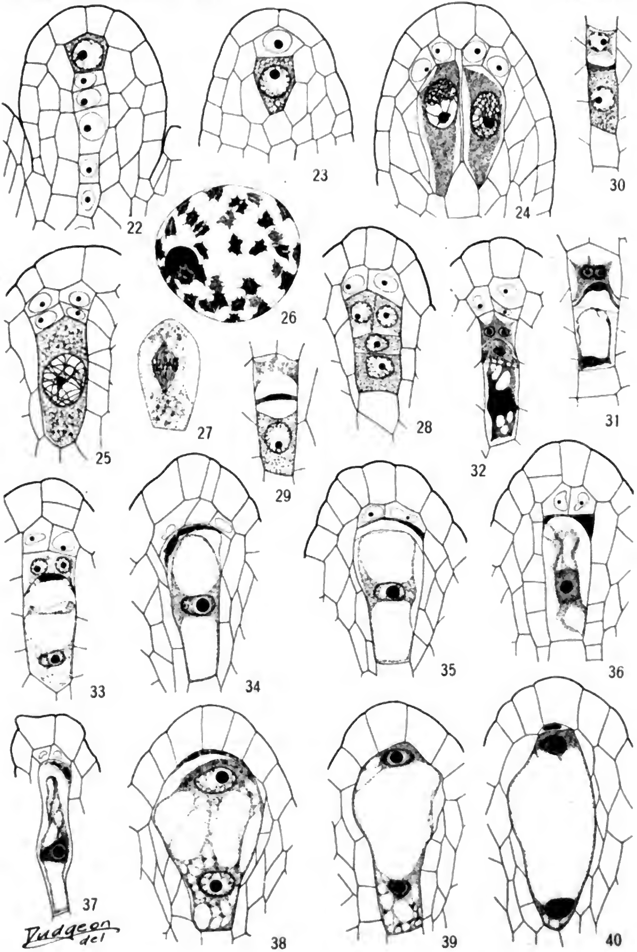
FIG. 71.—Hypertrophied pollen grain with contents in advanced disorganization.

FIG. 72.—Same, with beginning of pollen tube formation.

FIG. 73.—Hypertrophied pollen grain, with contents disorganized to homogeneous mass and beginning to collapse.

FIG. 74.—Portion of hypertrophied pollen grain with well developed pollen tube; disorganized nuclei still in grain.

FIG. 75.—Hypertrophied pollen grain with long pollen tube into which remains of disorganized nuclei have migrated.



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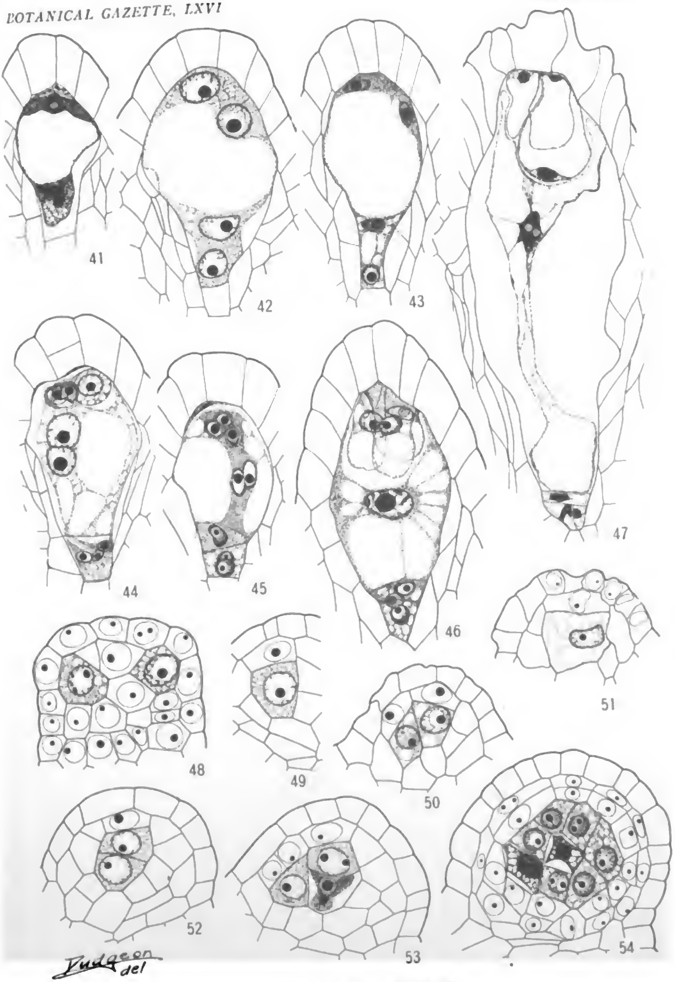

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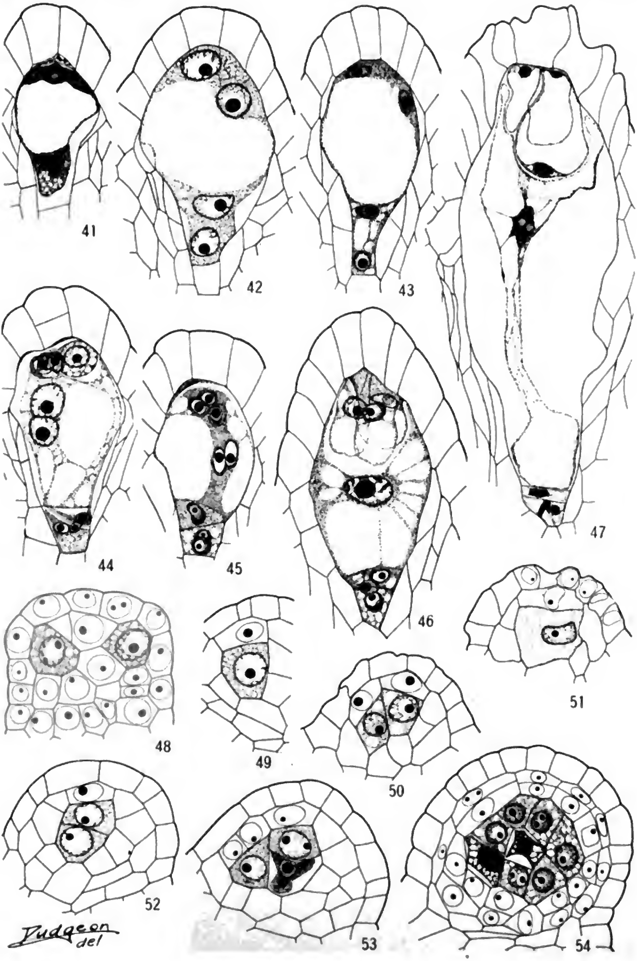

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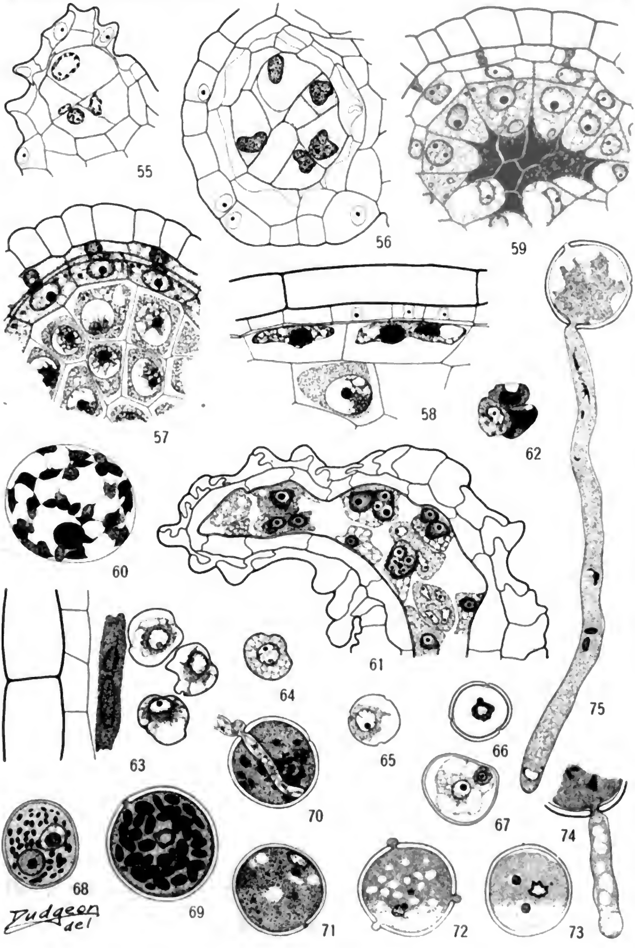

DUDGEON on RUMEX

NOTES ON NORTH AMERICAN TREES. III. TILIA. I

C. S. SARGENT

The results of a study of the lindens of the United States carried on for a number of years will be found in these notes. It is based on observations of these trees in the forest and the examination of a large collection of herbarium material gathered in all parts of the country where lindens grow.

To understand a species of *Tilia* properly 4 collections are needed: the first made in early spring to show the unfolding leaves, the second in early summer when the trees are in flower, the third 6 or 8 weeks later when the fruit is mature, and the fourth in winter for the winter buds. Many of these trees grow in regions where summer collecting presents many difficulties and causes much discomfort; the trees do not always flower every year, and the fruit often does not mature or is destroyed in storms before it is ripe. It is not surprising, therefore, that American lindens are poorly represented in the older herbaria and that botanists depending on collections in herbaria have not been able to obtain a comprehensive idea of the representatives of the genus in this country.

Even with abundant material it is difficult to find characters by which the different species and their varieties can be satisfactorily arranged. In most of the large genera of trees many of the species can be distinguished by the bark, but the bark of the American lindens varies so little that it has no value in determining species. The branchlets of some species are stouter than others, but stout and slender branchlets are often found on the same tree. Their color is uniform on some species, but on others varies from yellow or pale brown to red; on some species the branchlets are glabrous and on others they are pubescent, but in some species glabrous and pubescent branchlets are found on the same tree. In a few species a good character is found in the winter buds, but on other species the buds may be glabrous or pubescent. Except in size, there is no constant character in the flowers, and the fruit, although it varies slightly in size, is always globose, depressed-globose, slightly ovoid, or ellipsoidal, fruits of these different forms occurring in the same species and some of them on the same tree. The shape and size of the leaves vary on different branches of the same tree, but their serration and venation have sometimes specific importance. The only constant and reliable character, however, which I have found for distinguishing the species is in the absence or presence of the hairy covering on the surface of the leaves and in the nature of this covering when it exists, and the following arrangement of the species is based on these characters. The color of the hairs, however, cannot be depended on; on some species the hairs on the lower surface of the leaves are constantly white, but in other species they are brown or white on different trees, and on others they are white on the leaves of lower branches and brown on those of upper branches. When it is possible to make a comparative study of the trees growing together in an aboretum where they can be watched through the year it will probably be found that some of the characters which now seem constant cannot be depended on and that another arrangement of this group will be necessary.

Unfortunately the lindens first known from North America were described in Europe, often from cultivated trees, and the material on which these descriptions were made was insufficient and is often no longer in existence. There is therefore still some uncertainty in regard to the correct names of a few species.

I take this opportunity to express my sincere thanks to Mr. T. G. HARBISON, Professor R. S. COCKS, and Mr. E. J. PALMER, who have patiently and industriously collected *Tilia* material for the Arboretum and made possible these notes.

CONSPECTUS OF THE SPECIES OF THE UNITED STATES

Surface of the leaves glabrous at maturity.
  Leaves glabrous or almost glabrous when they unfold, coarsely serrate.
    Leaves furnished with conspicuous tufts of axillary hairs, their lower surface light green and lustrous; pedicels glabrous or nearly glabrous . 1. *T. glabra*
    Leaves usually without tufts of axillary hairs, their lower surface not lustrous; pedicels densely hoary tomentose . . . . 2. *T. nuda*

Leaves hoary tomentose when they unfold.

Leaves soon glabrous.

Leaves coarsely serrate with stout teeth, their veinlets conspicuous; branchlets stout, bright red . . . . 3. *T. venulosa*

Leaves finely serrate with straight or incurved teeth, their veinlets less conspicuous; branchlets slender, pale reddish brown . . 4. *T. littoralis*

Leaves crenately serrate, glaucescent on the lower surface 5. *T. creno-serrata*

Leaves covered below early in the season with articulate hairs, becoming glabrous or nearly glabrous.

Leaves thin, coarsely serrate, green or glaucescent on the lower surface, with or without tufts of axillary hairs; summer shoots not pubescent 6. *T. floridana*

Leaves subcoriaceous, finely serrate, bluish green and lustrous below early in the season; tufts of axillary hairs minute, usually wanting; summer shoots pubescent . . . . 7. *T. Cocksii*

Surface of the leaves pubescent below during the season.

Lower surface of the leaves covered with short gray firmly attached pubescence; tufts of axillary hairs not conspicuous . . . . 8. *T. neglecta*

Lower surface of the leaves covered with articulate easily detached hairs.

Branchlets without straight hairs.

Leaves ovate, acuminate, usually obliquely truncate at base, glabrous above, their pubescence brownish or white . . . . 9. *T. caroliniana*

Leaves oblong-ovate, cordate or obliquely cordate at base, pubescent above early in the season . . . . 10. *T. texana*

Leaves semiorbicular to broadly ovate, abruptly short-pointed, deeply and usually symmetrically cordate at base . . . . 11. *T. phanera*

Branchlets covered with straight hairs; leaves ovate, abruptly short-pointed, oblique and truncate at base . . . . 12. *T. lasioclada*

Surface of the leaves tomentose below during the season with close firmly attached tomentum.

Tomentum white, gray, or brown; leaves usually glabrous on the upper surface; branchlets and winter buds glabrous (occasionally pubescent in varieties of no. 13).

Branchlets slender; petioles not more than 4 cm. long; leaves oblong-ovate, acuminate or abruptly pointed, oblique and truncate or cordate at base; tomentum on the leaves of upper branches often brown; flowers 3.5–5 mm. long . . . . 13. *T. heterophylla*

Branchlets stout; petioles up to 7 cm. in length; leaves oblong-ovate, acuminate, obliquely truncate at base; tomentum always white; flowers 10–12 mm. long . . . . 14. *T. monticola*

Tomentum pale or brownish; leaves thickly covered above early in the season with fascicled hairs; branchlets tomentose; winter buds pubescent 15. *T. georgiana*

1. **TILIA GLABRA** Vent.—*Tilia americana* var. a *densiflora* V. Engler, Monog. Tilia, 137 (in part). 1909; *Tilia americana* var. *densiflora* f. *megalodonta* V. Engler, l.c. 139. 1909; *Tilia americana* var. *densiflora* f. *laxiflora* V. Engler, l.c. 140. 1909.—For the northern lime tree with glabrous leaves the name *Tilia americana* has been adopted in recent years by all authors who have written on American trees. LINNAEUS, however, based his species on the *Tilia floribus nectariis instructis* of KALM, quoting as synonyms of KALM'S species the *Tilia foliis majoribus mucronatis* of CLAYTON and the *Tilia amplissimis glabris foliis, nostrati similis* of PLUKENET Mant. 181. KALM'S specimen is not in the Linnaean Herbarium, and it is impossible to identify it from the description, which applies as well to anyone of the 3 species which KALM may have seen. Indeed both *T. neglecta* and *T. heterophylla Michauxii* are more common in the part of the country which he visited than the tree which recent authors have called *T. americana*, and it is impossible to identify KALM'S plant. CLAYTON'S description cannot be applied to the northern glabrous tree, for it is not known to grow in CLAYTON'S region; and as it is impossible to determine if more than one species was included in LINNAEUS' *T. americana* or, if the name was applied only to one species, what that species was, it seems necessary to give up entirely the name of *T. americana* Linnaeus. This name was taken up by MILLER in the eighth edition of *The Gardener's Dictionary*, but the leaves of MILLER'S *T. americana* are described as "subtus pilosis," and his species is probably the *T. neglecta* of SPACH, which is now known to be an old inhabitant of European gardens. AITON'S description in the *Hortus Kewensis*, "*T. floribus nectario instructis, foliis profundis cordatis argute serratis glabris*," well describes the northern glabrous tree, although he follows LINNAEUS in calling it a native of Virginia and Canada. The *T. caroliniana* of MARSHALL but not of MILLER is probably the northern tree, and his *T. americana* with leaves a little hairy underneath is evidently *T. neglecta*, which is the common species in MARSHALL'S region. If the *T. americana* of LINNAEUS is rejected, it is necessary to determine what name should be adopted for it. The next name used for this tree is *T. glabra* of VENTENAT, published in 1800, and this seems to be the name which should be adopted

for it, as it was by NUTTALL, DECANDOLLE, HOOKER, DARLINGTON, and other authors. In his description VENTENAT speaks of the leaves as "d'abord légerement pubescent, ensuite parfaitement glabre," which is correct, for although the young leaves are often entirely glabrous they are sometimes furnished for a few days after they unfold with scattered articulate hairs on the upper surface and on the lower surface with soft pale hairs which are most abundant on the midribs and veins.[1]

2. **Tilia nuda,** n.sp.—*Tilia pubescens* var. a *Aitonii* V. Engler, Monog. Tilia, 128 (in part). 1909; *Tilia americana* var. a *densiflora* V. Engler, l.c. 137 (insomuch as relates to Houston, Texas). 1909; *Tilia americana* probably of many authors but not of LINNAEUS.—Leaves thin, ovate, abruptly pointed at apex, obliquely truncate or unsymmetrically cordate at base, coarsely serrate with long, slender, straight, or slightly curved, conspicuously glandular teeth; as they unfold, dark red and sparingly pubescent on the midribs and veins, glabrous at the end of a few days, without or very rarely with small axillary tufts, dark green on the upper surface, pale yellow-green on the lower surface, 10–12 cm. long, 7–9 cm. wide; petioles slender, glabrous, 5–6 cm. in length. Flowers 8–10 mm. long, on hoary tomentose pedicels, in broad usually 10- or 12- sometimes 30- or 40-flowered long-branched glabrous corymbs; peduncle glabrous, the free portion 2–3 cm. in length, the bract glabrous, oblong, often slightly falcate, cuneate or rounded at base, rounded at apex, short-stalked, 1–3 cm. wide; sepals acute, rusty tomentose on the outer surface, glabrous on the inner surface; petals oblong-ovate, narrowed at the rounded apex; staminodia oblong-obovate, rounded at the broad apex, style glabrous. Fruit subglobose to depressed-globose, covered with rusty tomentum, 6–7 mm. in diameter.

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[1] VENTENAT'S paper on *Tilia* was read in 1799 and published in 1802 in the fourth volume of the *Mémoires de l'Acad. Sci. Paris*. A separate of this paper with the same pagination appeared the same year, but a Spanish translation without the illustrations was published in Madrid in May 1800 with the title *Monografia del género Tilo* in the second volume of the *Anales de Historia Natural*. The correct citation, therefore, of VENTENAT'S American species is *T. glabra* Ventenat in An. Hist. Nat. 2:62. 1800; *T. pubescens* Ventenat in An. Hist. Nat. 2:63. 1800; *T. pubescens* var. *leptophylla* Ventenat in An. Hist. Nat. 2:64. 1800; *T. heterophylla* Ventenat in An. Hist. Nat. 2:65. 1805.

Usually a small tree with pale furrowed or sometimes checkered bark, small spreading branches forming a narrow round-topped head, and slender glabrous orange or red-brown branchlets. Winter buds ovate, obtusely pointed, dull red, glabrous, 4–5 mm. long. Flowers usually in the first week of June before the other species with which it is associated. Fruit ripens in September.

MISSISSIPPI.—Rich woods and river bluffs near Natchez, Adams County, *Miss C. C. Compton*, June 2 and September 24, 1915 (no. 12 type), May and September 1915 (no. 13); Clifton Upper Bluff, *Miss Compton*, May 18, June 2, and September 24, 1915 (no. 2); Kingston Road, near Natchez, *Miss Compton*, August 26, 1915; Fenwick, Adams County, Miss *Compton*, April 17, 1915; bluff of the Mississippi River above Natchez, *C. S. Sargent*, April 8, 1913, April 17, 1915, and April 17, 1916; Woodville, Wilkinson County, *C. S. Sargent*, April 15, 1916; near Jackson, Hinds County, *T. G. Harbison*, May 17, 1915 (no. 63), September 19, 1915 (no. 63A), May 22, 1915, September 18, 1915 (nos. 84, 88A); Bolton, Hinds County, *T. G. Harbison*, May 24, 1915.

ALABAMA.—Hatcher's Creek, Berlin, Dallas County, *R. S. Cocks*, June 6, July 28, 1916 (no. 950).

LOUISIANA.—St. Francisville, West Feliciana Parish, *C. S. Sargent*, April 12, 1916; Lake Charles, Calcasieu Parish, *R. S. Cocks*, May 21, July 7, 1915 (no. 2530), May 21, 1915, *C. S. Sargent*, April 12 and 13, 1915, *E. J. Palmer*, May 16, September 11, 1915 (nos. 7644, 8523).

TEXAS.—White Oak Bayou, Houston, Harris County, *F. Lindheimer*, March 1840 (no. 10770 in Herb. Missouri Bot. Gard.), *E. J. Palmer*, May 17, September 15, 1917 (nos. 11397, 12763); Livingston, Polk County, *E. J. Palmer*, October 7, 1914 (nos. 6753, 6755), September 12, 1916 (no. 10696), April 4, September 17 and 19, 1917 (nos. 11467, 12016, 12796, 12797, 12798, 12803); Marshall, Harrison County, *E. J. Palmer*, October 17, 1914 (no. 6852), April 18, 1915 (no. 7277), June 8, 1915 (no. 7912); Larissa, Cherokee County, *B. F. Bush*, October 7, 1909 (no. 5977), *E. J. Palmer*, June 3, September 22, 1915 (nos. 7846, 8622); Liberty, Liberty County, *E. J. Palmer*, May 22, 1915 (no. 7736); San Augustine, San Augustine County, *E. J. Palmer*, September 7, 1916 (no. 10627); College Station, Brazos County, *E. J. Palmer*, April 28, 1917 (no. 11722); Huntsville, Walker County, *E. J. Palmer*, May 26, 1917 (no. 12046).

ARKANSAS.—Fulton, Hempstead County, *B. F. Bush*, April 5, 1909 (no. 5464A); McNab, Hempstead County, *E. J. Palmer*, June 18, 1915 (no. 8056), September 8, 1917 (no. 12674).

On this tree as it grows in the neighborhood of Natchez, where it is common, the bracts of the peduncles vary from 1 cm. up to 3 cm. in width. In *Miss Compton's* no. 12 the bracts are sometimes almost sessile or are borne on stalks of varying length up to 3 cm. At Larissa, Texas, trees growing on sandy moist hillsides are often 25–30 m. high, with trunks 75 cm. in diameter covered with deeply fissured bark. The absence of pubescence from the young leaves and the absence of axillary hairs well distinguish this species, but the absence of the axillary tufts cannot always be depended on, for occasional trees have been found in Louisiana and Alabama on which some of the leaves are furnished with these tufts (Louisiana, near Alexandria, Rapides Parish, *R. S. Cocks*, June 1905; Wakefield, West Feliciana Parish, *R. S. Cocks*, June 1905. Alabama, near Selma, Dallas County, *R. S. Cocks*, June and July 1914, June 2, July 12, 1915 [no. 784], April 20, July 25, 1916 [nos. 822, 960]).

A form of this tree with leaves more or less pale on the lower surface may be distinguished as

TILIA NUDA var. **glaucescens,** n.var.—Differing from the type in the glaucous lower surface of the leaves.

ALABAMA.—Bluffs of the Alabama River, Berlin, Dallas County, *R. S. Cocks*, June 11, July 20, 1915 (no. 786 type).

LOUISIANA.—Lake Charles, Calcasieu Parish, *R. S. Cocks*, May 21, 1915 (no. 2534); Natchitoches, Natchitoches Parish, *E. J. Palmer*, May 10, June 9, 1915 (nos. 7569, 7923), June 9, 1915 (no. 7923).

OKLAHOMA.—Page, Le Flore County, *E. J. Palmer*, July 27, 1917 (no. 12638).

TEXAS.—Marshall, Harrison County, *E. J. Palmer*, June 8, 1915 (nos. 7909, 7912); San Augustine, San Augustine County, *E. J. Palmer*, June 5, 1915 (no. 7880).

Like the green-leaved type, the trees of this variety differ in the size of the leaves, in the pedunculate bract which on *Palmer's* no. 7923 from Natchitoches is 8 cm. wide, while on his no. 7909 from Marshall it is only 3.5 cm. wide. The number of flowers in a corymb is equally variable. The tomentum on the fruit of *Cock's* no. 786 from Sardis, which is the only fruit of the variety which I have seen, is paler than that on the fruit of the green-leaved form.

TILIA NUDA var. **brevipedunculata,** n.var.—Differing from the type in the serration of its smaller leaves glaucescent below, in the shorter free portion of the peduncles of the inflorescence, and in its broader bract. Leaves ovate, gradually or abruptly narrowed and acuminate at apex, obliquely and unsymmetrically cordate or rounded at base, finely crenately serrate with gland-tipped teeth, smooth and dark yellow-green on the upper surface, pale yellow-green and glaucescent on the lower surface, glabrous, 7–8 cm. long and 5 or 6 cm. wide; petioles slender, glabrous, 2–2.5 cm. in length. Flowers 5 or 6 mm. long, on pubescent pedicels, in compact, mostly 10–20-flowered, sparingly pubescent corymbs; peduncle sparingly pubescent, the free portion only about 1.5 cm. in length, the bract broad and rounded or unsymmetrically cuneate at base, rounded or acute at apex, nearly sessile or short-stalked, glabrous with the exception of occasional fascicled hairs on the upper side of the midrib, 7–8 cm. long and 3–3.5 cm. wide, much longer than the peduncle; sepals acute, covered on the outer surface with pale pubescence and on the inner surface with soft white hairs; petals oblong-ovate, acuminate, a third longer than the sepals; staminodia obovate, gradually narrowed and cuneate at base, acute at apex. Fruit not seen.

A tree 8–10 m. high, with slender, glabrous, dark red-brown branchlets. Flowers the first week of June.

Flat wet woods subject to overflow, San Augustine, San Augustine County, Texas, *E. J. Palmer*, June 5, 1915 (no. 7889 type).

This tree should perhaps be considered the type of a new species. So little is known of it, however, that in spite of the different serration of the smaller leaves and the remarkably short free portion of the peduncle of the inflorescence and its broader bract, it is perhaps now best considered a variety of *T. nuda*, which is common in eastern Texas.

3. **Tilia venulosa,** n.sp.—Leaves broadly ovate, abruptly acuminate at apex, cordate or unsymmetrically cordate or obliquely truncate or cordate at base, coarsely serrate, with gland-tipped teeth pointing forward; when they unfold, covered with pale tomentum, soon becoming pubescent and glabrous before the flowers open, dark yellow-green on the upper surface, paler on the lower surface, 10–14 cm. long and broad, with prominent pale yellow midribs slightly villose on the upper side near the base, and 9 or 10 pairs of remote primary veins without axillary tufts and connected by conspicuous cross veinlets; petioles stout, glabrous, 4.5–5 cm. in length. Flowers 8–9 mm. long, on slightly pubescent pedicels, in broad, slender-branched, nearly glabrous corymbs; peduncle stout, glabrous, red, the free portion 2.5–4 cm. in length, the bract nearly sessile, oblong to slightly obovate, gradually narrowed and rounded at base, rounded at apex, glabrous on upper surface, pubescent below along the midrib and veins, 3–4 cm. wide, longer than the peduncle; sepals ovate, acute, pale pubescent on the outer surface, villose on the inner surface and furnished at the base with a tuft of long white hairs, a third shorter than the lanceolate acuminate petals; staminodia oblong-obovate, rounded at apex, about as long as the sepals; stigma slightly villose at base. Fruit sub-

globose, 6–7 mm. in diameter, covered with loose light brown pubescence.

A tree 20–25 m. high, with stout, red, glabrous branchlets. Winter buds ovate, cylindrical, obtusely pointed, dark red, 7–8 mm. in length. Flowers during the first week of July. Fruit ripens the end of September.

Rocky "coves" in rich soil, Hickory Nut Gap, in the Blue Ridge, North Carolina, *W. W. Ashe*, April, May, and October 1916 (distributed as *T. eburnea* Ashe), *T. G. Harbison*, July 5 and September 21, 1917 (no. 2 type for flowers, no. 3 type for fruit); near Saluda, Polk County, North Carolina, *T. G. Harbison*, July 4, 1917 (nos. 1, 2, 4, 5, 7).

TILIA VENULOSA var. **multinervis,** n. var.—Differing from the type in its obliquely truncate, not cordate, leaves with 12 or 13 pairs of more crowded primary veins, ellipsoidal fruit, slender branchlets, and smaller winter buds.

A single tree near Saluda, Polk County, North Carolina, *T. G. Harbison*, July 4 and September 20, 1907 (no. 6 type).

T. venulosa is one of the handsomest of the American lindens as it is one of the most distinct. Its relationship is with *Tilia glabra*, from which it differs in the venation of the more constantly cordate leaves without axillary tufts, tomentose when they unfold, in the bright red peduncles, in the red branchlets, and in the larger red winter buds.

4. **Tilia littoralis,** n.sp.—Leaves ovate, unsymmetrical and rounded on one side and cuneate on the other, or symmetrical and cuneate or oblique and truncate at base, abruptly short-pointed and acute or acuminate at apex, finely serrate with straight or incurved glandular teeth; when they unfold, covered above with scattered fascicled hairs and tomentose below, soon glabrous, and when the flowers open, thin, yellow-green, paler on the lower than on the upper surface, 8–10 cm. long and 4.5–6 cm. wide, with slender midribs and primary veins and small conspicuous tufts of rusty brown axillary hairs; petioles slender, glabrous, 2.5–3 cm. in length; leaves on young vigorous shoots broadly ovate, truncate or slightly cordate at base, more coarsely serrate, pubescent with fascicled hairs especially on the midribs and veins, 10–12 cm. long and 8–9 cm. wide, their petioles densely pubescent. Flowers 7–8 mm. long, on pale tomentose pedicels, in small, compact, mostly 9–15-flowered, pubescent corymbs; peduncle covered with scattered

fascicled hairs, the free portion 1.5–2.5 cm. long, the bract sessile, gradually narrowed and cuneate at base, rounded at apex, ciliate on the margins, pubescent on the midribs, otherwise glabrous, 8–10 mm. wide, longer or shorter than the peduncle; sepals acuminate, pale pubescent on the outer surface, villose on the inner surface along the margins and at the base with long white hairs; petals acuminate; staminodia oblong-obovate, rounded at apex. Fruit ellipsoidal to depressed-globose, apiculate, covered with pale brown tomentum, 6–7 mm. in diameter.

A tree with slender glabrous branchlets densely coated when they first appear with pale pubescence, soon glabrous, light reddish brown during their first summer, often bright red during their first winter, becoming purple the following year and ultimately light gray-brown. Winter buds ovate, glabrous or puberulous, bright red, about 5 mm. long and 2–3 mm. in diameter.

Shore of Colonel's, formerly Bermuda, Island on Dyke's Creek, an ocean inlet near the mouths of the North Newport and Medway rivers near Dunham, Liberty County, Georgia, *Miss Julia King*, August 1, 1915, *T. G. Harbison*, September 8 and 9, 1916 (nos. 3, 6, 7), June 18, 1917 (no. 15 type).

This species, which I only know from one locality, is distinct in its small leaves, which are often symmetrical and cuneate at base, and are entirely glabrous with the exception of small conspicuous tufts of axillary hairs, in the small pedunculate bract, slender branchlets, and minute winter buds.

TILIA LITTORALIS var. **discolor,** n.var.—Differing from the type in the smaller leaves (7–8 cm. long) glaucous on the lower surface.

A single tree 17 m. high with a trunk 20 cm. in diameter, leaning over a salt water creek, Colonel's Island, with trees of the typical form and "very conspicuous among the other lindens near by on account of its glaucous leaves," *T. G. Harbison*, June 16, 1917 (no. 16 type).

5. **Tilia creno-serrata,** n.sp.—*Tilia floridana* Sargent, Man. 672 (in part at least) (not Small) *fig. 548.* 1903.—Leaves ovate, abruptly narrowed and acuminate at apex, usually oblique and unsymmetrically cordate or truncate or occasionally symmetrical and cordate at base, crenately serrate, the teeth tipped with minute glands; when they unfold, covered with pale caducous tomentum; at maturity dark green and lustrous above, glabrescent below, glabrous with the exception of minute axillary tufts of rusty hairs, mostly 9–12 cm. long and 7–8 cm. wide; petioles slender, glabrous about 3 cm. in length. Flowers 7–8 mm. long, on hoary tomentose

pedicels, in compact, mostly 10–18-flowered, tomentose corymbs; peduncle glabrous, the free portion 2.5–4 cm. in length, the bract oblong-obovate, cuneate at base, rounded at apex, short-stalked, glabrous, usually about 2 cm. wide; sepals acute, hoary tomentose on the outer surface, coated with pale tomentum, mixed with long white hairs on the inner surface; petals narrow-acuminate; staminodia oblong-obovate, notched at apex. Fruit ellipsoidal, conspicuously apiculate at apex, rusty tomentose, 8–10 mm. long and 6–8 mm. in diameter.

A tree 8–10 m. high, with a trunk 25–30 cm. in diameter, and slender, glabrous, red-brown branchlets. Winter buds ovoid, acute, dark dull red, glabrous, 4–5 mm. long. Flowers the middle of June. Fruit ripens from the middle to the end of August.

FLORIDA.—Sandy woods, Oviedo, Seminole County (type locality), *T. L. Mead*, May 15, 1887, June 15 and August 29, 1910; Lake Charm, Orange County, *T. L. Mead*, May 15, 1887, June 1910, *T. G. Harbison*, May 28, 1917 (nos. 3, 4, 5, 6); San Mateo, Putnam County, *T. G. Harbison*, June 15 and September 8, 1915 (nos. 3, 3a, 13, 14); Gainesville, Alachua County, *T. G. Harbison*, June 10, September 10, 1915 (nos. 5, 5A); Lake City, Columbia County, *T. G. Harbison*, April 22 and June 17, 1917 (no. 8); Micanopy Junction, Alachua County, *R. M. Harper*, April 14, 1910 (no. 146); Sumner, Levy County, *T. G. Harbison*, June 12, 1915, June 15, 1916, April 25, June 15, September 25, 1917.

GEORGIA.—Albany, Dougherty County, *T. G. Harbison*, June 25, 1915.

Harbison's Gainesville specimens have more coarsely serrate oblong leaves up to 10 cm. in length and are oblique at base. The bract of the peduncle is 3 cm. broad and in the broader corymbs there are 40–50 flowers. The leaves, however, are crenately serrate and quite glabrous with the exception of the small axillary tufts. This is evidently only a vigorous branch. On one of *Harbison's* San Mateo specimens the leaves in shape and serration resemble those of his Gainesville plant and the pedunculate bracts vary from 1 to 2.5 cm. in width. In the other San Mateo specimen the pedunculate bract is only 1 cm. wide. On *Harbison's* Albany specimen the pedunculate bract is only 5 mm. wide. The trees at San Mateo, Sumner, and Gainesville grow in low hummocks in sandy soil and sometimes attain the height of 20 m., with trunks 45 cm. in diameter.

6. TILIA FLORIDANA Ashe. Fl. Southern U.S. 761. 1903.—*Tilia pubescens* var. a *Aitonii* f. *glabrata*, Engler, Monog. Tilia. 129 (in part). 1909; *Tilia caroliniana* var. *β floridana*, Engler, l.c. 132. 1909.—The typical form of this species from Jackson County,

Florida, has broadly ovate, coarsely serrate, thin, acuminate leaves cordate or on leading shoots oblique at base, light green above and pale or green and covered early in the season on the under surface with fascicled hairs which soon disappear, so that when the flowers open they are glabrous or almost glabrous; they are often without tufts of hairs in the axils of the veins, or when these occur they are small, but on trees growing west of the Mississippi River they are more conspicuous. The flowers are 5–6 cm. long and are borne on hoary tomentose pedicels in few-flowered, rather compact, pubescent corymbs; in length the pedunculate bract varies from 6 to 13 cm. and in width from 1.2 to 3.5 cm., and the fruit is subglobose and covered with rusty tomentum. It is a tree with slender, glabrous, red-brown or yellow branchlets and small, obtuse, glabrous winter buds.

From western Florida this linden ranges to northern Georgia and to North Carolina, through the Gulf states to Texas, and through Arkansas to eastern Oklahoma and northern Missouri.

NORTH CAROLINA.—Polk County, *W. W. Ashe*, June 1875 (no. 102).

GEORGIA.—Cornelia, Habersham County, *T. G. Harbison*, September 30, 1916 (no. 5); Albany, Dougherty County, *T. G. Harbison*, June 25, 1915 (no. 2); cliffs of the Savannah River above Augusta, Richmond County, *C. S. Sargent*, March 30, 1908, *T. G. Harbison*, April 16, 1916 (no. 7); Shell Bluff, 30 miles below Augusta, *C. S. Sargent*, April 6, 1914.

FLORIDA.—Jackson County, *T. G. Harbison*, September 18 and 19, 1916 (nos. 3, 5, 6, 9, 11); near Mariana, *T. G. Harbison*, April 20, May 26 and 29, and June 29, 1917 (nos. 1, 7, 8, 20, 25, 32); River Junction, Gadsden County, *T. G. Harbison*, September 14, 1915; Sumner, Levy County, *R. M. Harper*, April 26, 1909 (no. 35).

ALABAMA.—Birmingham, Jefferson County, *T. G. Harbison*, October 15, 1914, October 2, 1916, April 15 and May 18, 1917, April 4, 1918 (no. 24), June 24 and 28, 1918 (nos. 34, 35, 37, 40, 41, 42); Choctaw County, *C. Mohr*, August 20, 1880 (no. 55); Blount County, *T. G. Harbison*, October 13, 1906, September 23, 1915; Berlin, Dallas County, *R. S. Cocks*, June 25 and July 28, 1916 (nos. 950, 956).

MISSISSIPPI.—Yazoo City, Yazoo County, *T. G. Harbison*, May 1 and 30, 1915; near Natchez, Adams County, *C. S. Sargent*, April 1913, 1915, and 1916, *Miss C. C. Compton*, April, May, and September 1915; Jackson, Hinds County, *T. C. Harbison*, May 17, 24, and September 18, 1915 (nos. 64, 64a, 78, 78a, 113), *C. S. Sargent*, April 18, 1916; Bolton, Hinds County, *T. G. Harbison*, May 24, 1915.

Louisiana.—West Feliciana Parish, *R. S. Cocks*, May 15 and June 12, 1915 (nos. 2528, 2540); near Laurel Hill, *C. S. Sargent*, April 12, 1916; Welch, Beauregard Parish, *E. J. Palmer*, May 17, 1915 (no. 7673); near Opelousas, St. Landry Parish, *C. S. Sargent*, March 17, 1900, April 3, 1913; east of Opelousas, *R. S. Cocks*, April 3 and August 10, 1916 (nos. 4010, 4020); Lake Charles, Calcasieu Parish, *R. S. Cocks*, October 1914, May 21, 1915 (no. 2536), April 3, 1916 (nos. 2530, 4014), *E. J. Palmer*, May 19 and September 11, 1915 (nos. 7695, 8510, 8511); Winnfield quarries, Winn Parish, *R. S. Cocks*, April 18, 1917 (no. 4076); Shreveport, Caddo Parish, *R. S. Cocks*, June 1908 (no. 10), *E. J Palmer*, April 18 and September 6, 1916 (nos. 9479, 10608); sandy hills, Chopin, Natchitoches Parish, *E. J. Palmer*, April 21 and June 12, 1915 (nos. 7342, 7970); sandy upland woods, Natchitoches Parish, *E. J. Palmer*, May 10, 1915 (no. 7574); banks of Red River, Grand Ecore, April 15, 1916 (no. 9449).

Texas.—Marshall, Harrison County, *B. F. Bush*, October 8, 1901 (no. 993), *E. J. Palmer*, April 18, June 8, September 26, 1915 (nos. 7279, 8675); Houston, Harris County, *E. J. Palmer*, May 17, September 15, 1915 (nos. 11937, 12763); Livingston, Polk County, *E. J. Palmer*, April 9, 1914 (no. 5151), May 23, 1917 (no. 12003); Pledger, Matagorda County, *E. J. Palmer*, May 8, 1916; Larissa, Cherokee County, *E. J. Palmer*, June 3, September 22, 1915 (nos. 7844, 8619), April 7, September 14 and 16, 1916 (nos. 9373, 9377, 9382, 9387, 10706, 10707, 10709); Groesbeck, Limestone County, *E. J. Palmer*, June 1, 1915 (no. 7833); San Augustine, San Augustine County, *E. J. Palmer*, June 5, 1915 (nos. 7882, 7883), April 19, September 8, 1916 (nos. 9487, 9491, 9498, 10635, 10637), September 9, 10, 1917 (nos. 10730, 12689, 12690); Palestine, Anderson County, *E. J. Palmer*, September 15, 1916, May 29, 1917 (nos. 12085, 12086); Dayton, Liberty County, *E. J. Palmer*, April 3, May 21, 1917 (nos. 11461, 11977); Huntsville, Walker County, *E. J. Palmer*, May 24, 1917 (no. 12024); rocky banks of the Blanco River, Blanco County, April 4, June 5, September 25, 1917 (nos. 11577, 11578, 11579, 11580, 12160, 12164, 12166, 12167, 12171, 12860, 12861, 12866), April 5, 1918 (nos. 13281, 13286); near Boerne, Kendall County, *S. H. Hastings*, June 23, 1911 (no. 201), *E. J. Palmer*, March 27, May 19 and 26, September 27, 1916 (nos. 9265, 9812, 9813, 9823, 9824, 9876, 9879, 9889, 10823, 10824), April 6 and 19, June 13 and 16, September 28–30, 1917 (nos. 11473, 11477, 11485, 11490, 11493, 11594, 11597, 11603, 12239, 12240, 12241, 12243, 12278, 12890, 12897, 12898, 12905); base of the bluff of the Guadalupe River, Kerrville, Kerr County, *E. J. Palmer*, April 8, May 27, June 9, 1917 (nos. 9930, 11503, 12212, 12215, 12216), May 16, 1918 (no. 13269); Lacey's Ranch, near Kerrville, *E. J. Palmer*, May 31, June 6 and 10, July 3, 1916 (nos. 9957, 10032, 12221), April 8, 1917 (no. 11495); rocky banks, upper Seco Creek, Bandera County, *E. J. Palmer*, May 18, 1916 (no. 10236); rocky banks of the Frio River, Concan, Uvalde County, June 14, 1916 (nos. 10183, 10200), April 13, 1917 (nos. 11541, 11542).

ARKANSAS.—Fulton, Hempstead County, *B. F. Bush*, April 11, 1905 (no. 2290), April 28, May 19, June 6 and 10, October 4, 1909 (nos. 5543, 5647B, 5780A, 5814, 5815, 5926), *J. H. Kellogg*, June 20, 1910, *E. J. Palmer*, April 22 and 23, October 19, 1914 (nos. 5355, 5365, 6876), April 10, June 17, 1915 (nos. 7179, 8044), July 18, 1916 (no. 10513); McNab, Hempstead County, *E. J. Palmer*, April 12, June 18, 1915 (nos. 7187, 7204, 8054), April 8, 1916 (no. 9401); Brentwood, Washington County, *E. J. Palmer*, July 7, 1914 (no. 8214); Gum Springs, Clark County, *E. J. Palmer*, June 20, 1915 (no. 8073), July 21, 1916 (nos. 10539, 10543, 10544); Piney, Johnson County, *E. J. Palmer*, June 30, 1915 (no. 8161); Ashdown, Little River County, *E. J. Palmer*, July 21, 1915 (no. 8367); Fort Lynn, Miller County, *E. J. Palmer*, July 19, 1916 (no. 10529); Van Buren, Crawford County, *G. M. Brown*, June 1908; Rogers, Benton County, *B. H. Slavin*, April 30, 1910; Cotter, Marion County, *E. J. Palmer*, September 1, 1915 (no. 804).

OKLAHOMA.—Lenapah, Nowata County, *G. W. Stevens*, August 19, 1913 (no. 2171); near Page, Le Flore County, *G. W. Stevens*, September 8, 1913 (no. 2669), *E. J. Palmer*, October 28, 1915 (no. 9033); Poteau, Le Flore County, *E. J. Palmer*, July 13, 1915 (no. 8281); Fort Towson, Choctaw County, *E. J. Palmer*, July 10, 1915 (no. 8307); Idabelle, McCurtain County, *E. J. Palmer*, July 22, 1915 (no. 8382); Antlers, Pushmataha County, *E. J. Palmer*, July 17, 1915 (no. 8339).

MISSOURI.—Hannibal, Marion County, *J. Davis*, June 5, 1914; Clarksville, Pike County, *J. Davis*, June 16, 1914; Allenton, St. Louis County, *C. S. Sargent*, April 4, 1909; Siebert's Mill, *E. J. Palmer*, August 5, 1916 (no. 10572); Williamsville, Wayne County, *E. J. Palmer*, June 29, 1914 (no. 6126); near Mansfield, Douglas County, *E. J. Palmer*, July 10, 1914 (no. 6254); Elk Springs, McDonald County, *E. J. Palmer*, May 3, 1914 (no. 5473); Galena, Stone County, *E. J. Palmer*, May 20, 1914 (no. 5648), July 25, 1916 (nos. 10561, 10566); Noel, McDonald County, *B. F. Bush*, April 25, October 8, 1909 (nos. 5530, 5983); Eagle Rock, Barry County, *B. F. Bush*, August 10, 1905 (no. 3211), *E. J. Palmer*, July 17, 1914 (no. 6311).

MEXICO.—Coahuila, *Ed. Palmer*, 1880 (no. 118 in Herb. U.S. Nat. Mus.); mountains near Monclova, *Ed. Palmer*, August 19, 1880 (no. 118 in Herb. U.S. Nat. Mus.).

The specimen collected by *Edward Palmer* on the mountains west of Monclova in the state of Coahuila August 19, 1880 (no. 118), and distributed as *T. mexicana* Bentham cannot be distinguished from specimens from western Texas which I have referred to *T. floridana*. *T. mexicana* of BENTHAM (Pl. Hartweg. 35. 1839) is said to have come from the neighborhood of Anganguio in the state of Michoacan in southern Mexico and not to be the same as the earlier *T. mexicana* Schlechtendal (Linnaea 11:37. 1837) collected near Chiconguiaco in the state of Hidalgo, and by HEMSLEY doubtfully referred to *T. americana* Linnaeus. *T. mexicana* Bentham is a nomen nudum.

A variety of this tree which differs only in its glabrous corymbs and puberulous peduncles may be distinguished as

TILIA FLORIDANA var. **australis,** n.var.—*Tilia australis* Small, Flora Southern U.S. 761. 1903; *Tilia pubescens* var. a *Aitonii* f. *glabrata* V. Engler, Monog. Tilia, 129 (in part). 1909.

This variety I have seen only from Blount County, Alabama.

Another linden of this group had best perhaps be considered as a variety of *T. floridana*, distinguished in the shape of its leaves and in their more prominent tufts of axillary hairs. I suggest for the name of this variety

TILIA FLORIDANA var. **oblongifolia,** n.var.—Distinguished from the type by its ovate-oblong leaves with more conspicuous tufts of axillary hairs. Leaves thin, ovate-oblong, long-pointed and acuminate at apex, unsymmetrical and rounded on one side and broadly cuneate on the other, or very oblique and truncate at base, coarsely serrate with apiculate teeth, dark green, smooth and lustrous on the upper surface, glaucescent or pale green on the lower surface, and furnished with usually large conspicuous tufts of axillary hairs, 8–10 cm. long and 6–8 cm. wide; petioles slender, glabrous, 3–4 cm. in length. Flowers 5–6 mm. long, on slender, hoary tomentose pedicels, in wide, thin-branched, stellate-pubescent, mostly 15–20-flowered corymbs; peduncle slender, glabrous, the free portion 2–2.5 cm. long, the bract acuminate at base, rounded at apex, raised on a slender stem, 1.3–1.5 cm. wide, much longer than the peduncle; sepals acuminate, hoary tomentose on the outer surface, villose at the base and along the margins on the inner surface; petals narrow, acuminate, nearly twice as long as the sepals; staminodia narrow spathulate, rounded and erose at apex, about as long as the petals; stigma slightly villose at base. Fruit on slender pubescent pedicels, ellipsoidal, covered with pale brownish tomentum, 6–7 mm. long and 5–6 mm. wide.

A tree with slender, glabrous, pale reddish brown branchlets, becoming dark red-brown in their second year. Winter buds obtuse, glabrous, 4–5 mm. in length. Flowers early in June. Fruit ripens at the end of July.

FLORIDA.—Blue Springs, Jackson County, *T. G. Harbison*, September 18, 1916; River Junction, Gadsden County, *T. G. Harbison*, April 25, 1914 (no. 1478), June 7, 1915 (no. 26); Tallahassee, Leon County, September 12, 1915 (no. 2a); San Mateo, Putnam County, *T. G. Harbison*, June 15, 1915 (no. 2).

ALABAMA.—Bluffs of the Alabama River, near Berlin, Dallas County, *R. S. Cocks*, June 5 and July 25, 1915 (no. 788 type), April and June 1916 (nos. 820, 832, 834, 952, 954, 958), June 3 and 31, 1917 (nos. 1200, 1202, 1204), *C. S. Sargent*, April 19, 1915.

MISSISSIPPI.—Edwards, Hinds County, *T. G. Harbison*, May 18, 1915 (no. 15); near Jackson, Rankin County, *T. G. Harbison*, May 20, 1915 (no. 76); Natchez, Adams County, *C. S. Sargent*, April 17, 1915.

LOUISIANA.—Laurel Hill, West Feliciana Parish, *R. S. Cocks*, March 1910; Avery Island, Iberia Parish, *R. S. Cocks*, May 29 and July 28, 1916 (nos. 4042, 4052); sandy woods, Natchitoches, Natchitoches Parish, *E. J. Palmer*, June 11 and September 27, 1915 (nos. 7056, 8699), April 13 and 14, 1916 (nos. 9416, 9437), June 11 and September 25, 1915 (nos. 7956, 8437, 9416), April 1916, Grand Ecore, May 5, 1915 (no. 7523); Chestnut, *E. J. Palmer*, April 17, 1916 (no. 9462).

ARKANSAS.—Fulton, Hempstead County, *B. F. Bush*, April 11, 1905 (no. 7534 in Herb. Mo. Bot. Gard.); Benton, Saline County, *E. J. Palmer*, June 24 and September 3 and 6, 1915 (nos. 2128, 8129, 8131, 8447, 8479), July 22, 1916 (nos. 10546, 10547, 10548, 10552).

TEXAS.—Marshall, Harris County, *E. J. Palmer*, April 18, June 8 and September 26, 1915 (nos. 7278, 7910, 7913, 8674); Palestine, Anderson County, *E. J. Palmer*, May 29, 1917 (no. 12086); Livingston, Polk County, *E. J. Palmer*, April 3 and May 23, 1917 (nos. 11468, 12003, 12004, 12014).

In *Tilia* a fairly constant specific character can usually be found in the absence or presence of the tufts of hairs in the axils of the leaves, but in *T. floridana* they are usually small and sometimes wanting in what is here considered the typical form of the species from western Louisiana; but westward, especially in Texas and Arkansas, they are usually present and sometimes conspicuous, as they are generally on the leaves of the var. *oblongifolia*, and it is only by the narrower more elongated leaves that this variety can be distinguished. The leaves of *T. floridana* have been described as glaucous on the lower surface, but this is not a constant character, as on the same branch leaves glaucescent and green below often occur. A variety of this species with leaves covered below with a silvery white bloom may be distinguished as

TILIA FLORIDANA var. **hypoleuca**, n.var.

ARKANSAS.—At the foot of a high bluff growing on the rocky margin of White River or on talus sloping to the foot of the bluff in rich soil across the river from Cotter, Marion County, *E. J. Palmer*, June 12, 1914 (no. 5943 type), July 24, 1916 (nos. 10555, 10559).

MISSOURI.—Galena, Stone County, *E. J. Palmer*, October 10, 1913, July 25, 1916 (nos. 4616, 10565); Branson, Taney County, *E. J. Palmer*, June 8, 1914 (no. 5896).

The unusual whiteness of the under surface of some of the leaves of this variety is due to a thick bloom. When this is rubbed off, the surface left is pale green. This bloom appears to be most common on leaves near the ends of branches and is often entirely wanting from those lower down on the branches and from the leaves of young vigorous shoots.

7. **Tilia Cocksii,** n.sp.—Leaves ovate, abruptly acuminate at apex, very oblique at the truncate or rounded base, dentate with small, remote glandular apiculate teeth; when they unfold covered with loose floccose pubescence, nearly glabrous when fully grown early in April; when the flowers open, dark green, and lustrous on the upper surface, pale blue-green and lustrous below, and at midsummer when the fruit ripens, subcoriaceous, dark green and lustrous on the upper surface, paler on the lower surface with slender primary veins without or occasionally with minute axillary tufts, and connected by conspicuous straight or curved veinlets, 9–10 cm. long and 6–7 cm. wide; petioles slender, glabrous, 1.5–2.5 cm. in length; leaves on leading summer branchlets sometimes obliquely cordate, more coarsely serrate, covered on the upper surface with short fascicled hairs, and floccose-pubescent on the lower surface, 10–13 cm. long, 10–12 cm. wide, their petioles puberulous. Flowers 6–7 mm. long, on tomentose pedicels, in compact pubescent many-flowered corymbs; peduncle slender, glabrous, the free portion only 1.5–2 cm. in length, the bract oblong, occasionally slightly obovate, rounded at the ends and sessile, hoary tomentose on the under surface and pubescent on the upper surface when it first appears, and when the flowers open puberulous below and glabrous above, 1.2–1.5 cm. in width and much longer than the peduncle; sepals ovate, acuminate, pale pubescent on the outer surface, villose at the base on the inner surface, a third shorter than the lanceolate acuminate petals; staminodia oblong-obovate, rounded at apex, about half the length of the petals; style glabrous. Fruit globose to depressed-globose, covered with loose brown tomentum, 6–7 mm. in diameter.

A small tree with slender, dull red, glabrous branchlets, the leading branchlets in summer more or less pubescent. Winter buds ovate, acute, dull red, glabrous or pubescent on leading shoots, 5–6 mm. long. Flowers the middle of May. Fruit ripens the middle of July.

Bank of the Calcasieu River, West Lake Charles, Calcasieu Parish, Louisiana, *Sargent* and *Cocks*, March 23, 1917, *R. S. Cocks*, May 15 and July 12, 1918 (no. 4922 type for flowers, 4949 type for fruit); low woods, Lake Charles, Calcasieu Parish, *C. S. Sargent*, March 26, 1911, April 12 and 13, 1915.

From other American lindens *T. Cocksii* differs in the thicker dark green lustrous leaves, in the peculiar bluish color of their lower surface in early spring, and in the pubescence during the summer on the leaves and branchlets of leading shoots in a species which, except when the leaves unfold and the inflorescence first appears in early spring, is otherwise glabrous. It is most closely related to *T. floridana*, from which it differs in the texture, color, and venation of the more finely serrate leaves, in the more compact inflorescence, and in the much shorter free portion of the peduncle. I take much pleasure in associating with this handsome tree the name of Professor REGINALD WOODHOUSE SOMERS COCKS, professor of botany in Tulane University and for many years my companion in annual journeys of exploration through the forests of Louisiana.

ARNOLD ARBORETUM
JAMAICA PLAIN, MASS.

PINE NEEDLES, THEIR SIGNIFICANCE AND HISTORY

JEAN DUFRENOY

(WITH TWENTY-NINE FIGURES)

Are pine needles shoots or leaves? The question may still be debated, since neither the shoot nor the leaf has as yet been clearly defined. A review of the morphology, development, and physiology of the "needles" may be of interest.

Morphology

The definition given by VAN TIEGHEM (**21**), and usually adopted, is as follows: The leaf is symmetrical on both sides of a plane; the shoot is symmetrical around an axis. A needle is symmetrical on both sides of a plane, not around an axis; but by bringing into contact the different needles grouped at the end of a spur shoot, an organ is obtained which is symmetrical around an axis, and which therefore is a shoot. Needles, therefore, are fragmentary shoots. Anatomically they are polystelic shoots which have divided longitudinally into a variable number of parts[1] in order to increase the surface available for carbon assimilation. Being fragmentary shoots, the needle may be considered the homologue of the petiole of broad-leaved gymnosperms. The anatomy of the needle is strikingly similar to that of the petiole in *Ginkgo*, and we may quote COULTER (**4**) as follows: "The most ancient gymnosperms possessed ample fernlike leaves. . . . . The conifers, however, have developed a very different type of leaf . . . . which reaches an extreme expression in small and rigid needles."

The derivation of needles from fernlike phyllodes is apparent from anatomical data.

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[1] That the different needles of a spur shoot are parts of the same organ is often strikingly evident. In most cases when a needle bends, the others bend also, so that all can be grouped into a cylindrical, though bent, shoot. When solitary, at the end of a spur shoot, needles are roughly cylindrical in form and shootlike, as normal needles of *P. monophylla*, and abnormal needles of *P. Pumilio* (STRASBURGER), *P. Laricio* (BOODLE **1**), and *P. maritima* (DUFRENOY **13**).

1. RELATION OF PINES TO CYCADS.—"Inverse wood," such as occurs in the petioles of cycads, may be demonstrated on the ventral side of the protoxylem in juvenile leaves and needles of

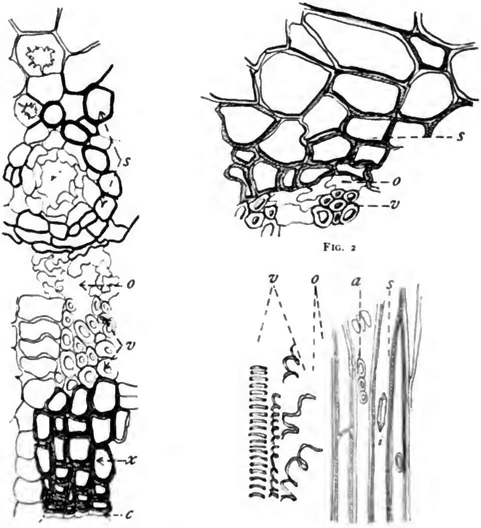

FIG. 1

FIG. 2

FIG. 3

FIGS. 1–3.—Transfusion sheath in needles of *Pinus maritima** (needle 2 years old, collected May 5, 1918, section 5 mm. above base): fig. 1, part of wood in vascular bundle; *c*, cambium, still dormant; *x*, wood of second year, vessels staining deep red with phloroglucin; *v*, wood of first year (protoxylem), spiral vessels, not staining with phloroglucin; *o*, lacuna; *s*, inverse wood, staining light red with phloroglucin, bright green with methyl green, orange with Sudan III; r^1, resin canal; fig. 2, detail of inverse wood (shaded tissue *s*), showing relation to protoxylem (*v*) and to pitted cells of periderm; *o*, lacuna; fig. 3, longitudinal section of same, showing spiral vessels of protoxylem (*v*) and inverse wood (*s*); *o*, lacuna; *a*, pitted vessels; *i*, oxalate of calcium.

* All the figures are from *Pinus maritima* collected at Arcachon.

P. maritima.[2] In normal needles, however, it is restricted to a few elongated vessels, sparsely distributed among pitted cells, from which they can be easily differentiated. They are always associated with peculiar elongated vessels which stain a bright orange with Sudan III (figs. 1–4). Tumors of **Coccus resinifians,** n. sp.,[3] however, may result in the reversion of the vascular strand in the infected needles to the cycad structure, through the development of a well defined bundle of inverse wood, which may often extend from the ventral face of the protoxylem to the endodermis (figs. 5–16).[4]

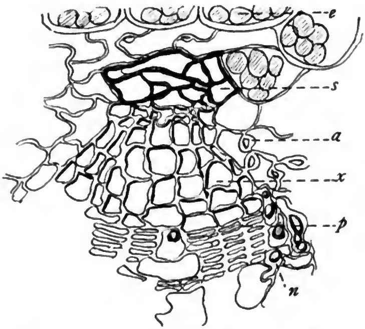

FIG. 4.—Part of periderm of young juvenile leaf (collected May 1918): *p*, phloem, with medullary rays (*n*) crowded with resin drops; *x*, normal wood; *s*, inverse wood in transfusion sheath, staining orange with Sudan III; *e*, endodermis.

2. RELATION OF PINES TO FERNS.—Other tumor-infected needles show phloem differentiating on the dorsal side of the inverted

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[2] VAN TIEGHEM considered the transfusion sheath on the ventral side of normal wood in pine needles to be the homologue of the "inverse wood" in the petiole of cycads. Following TAKEDA (**19**), we found this untenable.

[3] This *Coccus* has been recorded by DUFRENOY from stem tumors of pines, but the name was omitted from the note (**13**).

[4] Stomatal anatomy also emphasizes the origin of cycads and pines from a common stock (REHFOUS **18**)

bundle of xylem, resulting in a fernlike state, comprising two bundles of xylem facing each other, with phloem outside (fig. 7). The relation of pines to the fern stock is further emphasized by the occurrence (in the wood or periderm of tumor needles) of all transitional forms, from normal pitted elements to scalariform cells, such as are present in ferns, and restricted to endodermal cells of normal needles.[5]

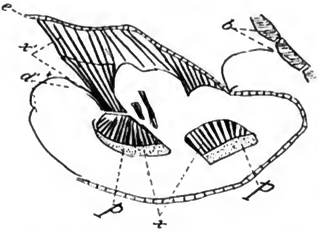

FIG. 5.—Tumor of *Coccus resinifians* on pine needle (collected at Arcachon, dunes of Abatilles, June 1917): part of periderm (schematic); *e*, endodermis, crowded with starch grains (starch and resin are much more abundant in tumor than in sound neighboring tissue); d^1, lignified cells of hyperplasia due to infection by *Coccus; b*, epidermis and hypoderm; *x*, normal wood; *p*, phloem; x^1, inverse wood, composed of sclerenchymatous cells and fibers (staining red with eosin and green with methyl green) and of vessels staining orange with Sudan III; this inverse wood develops from ventral face of protoxylem to endodermis, and is homologous with inverse wood in cycads.

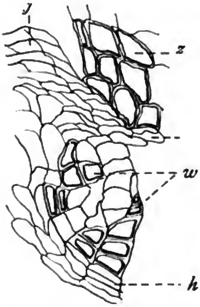

FIG. 6.—Part of fig. 5: *h*, phloem; *w*, lignified vessels in normal wood; *z*, same in inverse wood; *j*, lignified cells with hyperplasia.

3. RELATION OF PINES TO GNETALES.—Scalariform cells in pine needles may be compared to the tracheae in Gnetales, and suggest the origin of both from a common fern stock.

4. RELATION OF PINES TO EQUISETALES.—The origin and evolution of the protoxylem is strikingly similar in pine

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[5] The perforations in the scalariform cells of pines may be explained as derived from the fusion of enlarged bordered pits, as claimed by THOMSON for Gnetales; but the reverse is probably true, bordered pits being derived from ancestral simple incomplete perforations by acquiring highly specialized characters.

needles and in the stems of *Equisetum*, as it differentiates in both centripetally, from "pôles ligneux," and partially dissolves into lacunae.

The reappearance of polystelic organs, where the stele shows two vascular strands with opposed xylem and peripheral phloem, is fundamental in indicating the origin of conifers from a fern stock. The cycad stele may be derived from the fern stele by suppression of phloem in one of the two vascular strands, the remaining xylem bundle being the so-called "inverted wood." If this inverted wood itself almost entirely disappears, then the normal state of the pine needle is obtained.

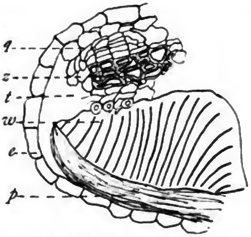

FIG. 7.—Half of vascular strand in tumor needle (collected November 1917): *e*, endodermis; *t*, periderm; *w*, normal wood; *p*, normal phloem; *z*, inverse wood; *q*, phloem.

Development

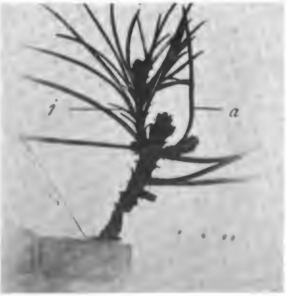

FIG. 8.—Proliferating spur shoots, springing up between the two geminate needles (*a*); *j*, juvenile leaf with spur shoot in axil.

REJUVENESCENCE AND JUVENILE LEAVES.—Whenever a resting organ grows again, rejuvenescence must take place, and this is always observed in pines, either at the germination of the seed, or when lateral, dormant buds are caused to develop pathologically. When the pine seed germinates, cotyledons develop on the young shoot, and then single juvenile leaves. These are smaller the higher up the shoot they develop, and at a certain height they are mere scale leaves. It is at the base of these scales that the spur shoot of the needles arises. After it has developed a few scale leaves and a tuft of needles, this spur shoot generally remains dormant. If, however, the terminal bud of a branch happens to die, these lateral shoots may grow into a normal branch, bearing at first isolated juvenile green leaves and then scale leaves with spur shoots in their axils (fig. 8).

VARIATIONS IN THE NUMBER OF NEEDLES.—The number of needles on the spur shoot of each species is considered constant enough to be used as a character for classification; still, on rejuvenated or infected twigs, shoots are found which bear an unusual number of needles. BOODLE (**1**) makes the following statement: "In *Pinus monophylla* the spur shoots as a rule bear each a single needle, but two are occasionally present. MASTERS found by studying early stages that two leaf rudiments are always produced, but that one of them generally becomes arrested at an early stage."

Single needles have been observed by BOODLE on *P. Laricio*, and we found some on twigs of *P. maritima* that were infected by the larva of a xylophage insect (*Hylesinus piniperda*). These single needles are roughly cylindrical; in many cases a groove is present on one side of the leaf. On following it downward, it is found to contain two papillae, one of which is the apex of the spur shoot, the other the rudiment of the second needle. Variation in the number of needles in this case is due to arrest in the development of one of them. It is a rare occurrence in *P. maritima* and *P. Laricio*, but it has become the rule in *P. monophylla*. The multiplication of needles on the spur shoot has often been recorded on wounded, infected (**13**), or vigorous (**20**) shoots, and it has been regarded as a reversion toward ancestral, many-leaved gymnosperms (**3**).

Although these variations are somatic in origin, we have proved that they comply with Mendel's law, in that the proportion of bud mutations on the shoot is precisely that of F_2 recessives in the case of hybrids. Shoots of vigorous *P. maritima* or those infected with *Coccus resinifians* have been observed to yield 75 per cent normal 2-needled spur shoots, and 25 per cent 3-needled spur shoots. Proliferating spur shoots on *P. virginica* in Arcachon often yield 75 per cent normal 3-needled spur shoots, and 25 per cent abnormal

2-needled spur shoots, or vice versa (**14**). These bud mutations, like proliferating spur shoots,[6] are due to modifications in the normal nutrition of the pine, caused by environmental factors, traumatisms, and chiefly parasites, and they result in increase of osmotic pressure in differentiating tissues.

That osmotic pressure is the ultimate determining factor is demonstrated by the fact that we were able to force 7-year old *P. maritima* to produce 3-needled spur shoots or proliferating spur shoots by watering abundantly, which of course increased turgescence of cells. Whether needles or juvenile leaves develop depends upon the relative supply of soluble osmotic material to the cells. Needles, or all adult organs in general, develop from material obtained from the earth and atmosphere, by gradual assimilation. Juvenile leaves, or all juvenile organs in general, develop from material stored in the reserve tissue (**9**).

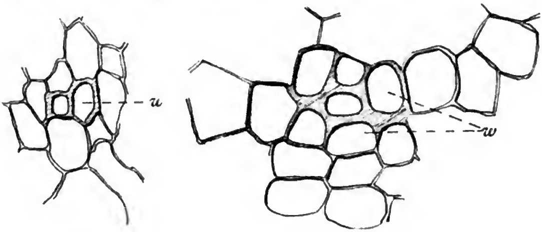

FIG. 9 FIG. 10

FIGS. 9–10.—Fig. 9, protoxylem in first needle appearing on juvenile pine: *w*, cells whose walls begin to show lignification and stain red with phloroglucin; fig. 10, protoxylem in very young needle of juvenile pine: section near apex; only one xylem pole.

TRANSITION FROM JUVENILE LEAVES TO NEEDLES.—As needles and juvenile leaves are but different responses of the same organism to environmental factors, they may be assumed to show transitional forms (contrary to the opinion of DAGUILLON 5). In fact, transitions are observed. The first needle to appear on juvenile pines shows anatomical features of juvenile leaves (figs. 9–17); and

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[6] Development of lateral long shoots is exaggerated on pine seedlings exposed to sea wind, and results in "buissornement," like that recorded by DEVAUX (**6**) for *Erica* on ocean dunes.

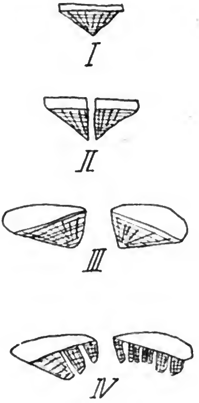

FIG. 11

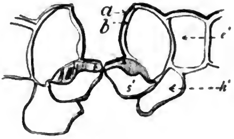

FIG. 12

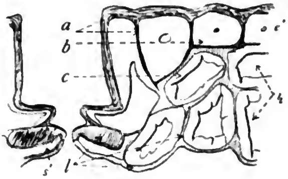

FIG. 13

FIGS. 11–13.—Fig. 11, transition from one vascular bundle to two semi-bundles in successive transverse sections from apex to base of needle: primary wood at apex (I) grouped into one bundle and like wood in juvenile leaves or in leaves of ancestral gymnosperms; with secondary structure, wood divides into two fragmentary bundles and becomes more like that in shoot (II–IV); fig. 12, stomatal cells of first needle produced on juvenile pine, showing structure of stomatal cells in juvenile leaves: no hypodermal cell present except below stomatal cells; letters as in fig. 13; fig. 13, stomatal and epidermal cells of needle on adult pine: *a*, cutin, staining orange with Sudan III; *l*, lignin, staining red with phloroglucin; *b*, thickening of epidermal cells, staining green with cotton blue; *c*, thickening of hypodermal cells; *h*, hypoderm; e^1, epidermis; s^1, stomatal cell (note local thinning of lignified wall, forming hinges).

transitions from one vascular bundle (as shown in juvenile leaves) to two semi-bundles (as typical of needles) is observed in successive sections of needles from the apex downward (fig. 11).[7] Needles

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[7] The anatomy of needles varies so much from apex to base as to make all comparison worthless unless distance of the transverse section from the apex be clearly stated. The same statement applies to the age of the needle and the season when material is collected.

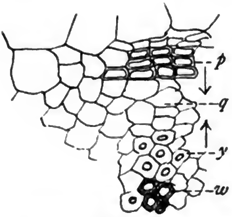

FIG. 14

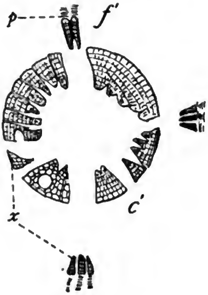

FIG. 15

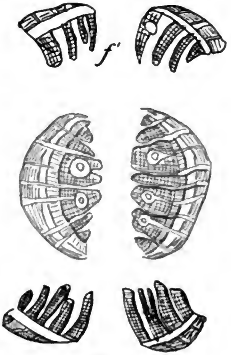

FIG. 16

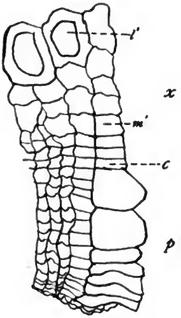

FIG. 17

FIGS. 14–17.—Fig. 14, periderm of very young juvenile leaf (collected April 25, 1918): *w*, protoxylem; *p*, phloem; *y*, cells of future wood beginning to lignify; *q*, procambium; arrows indicate direction of differentiation; wood first differentiates centripetally and procambium becomes more narrow until finally it is a mere band of cambial cells; note identity of procambium in juvenile leaves and in first needles of juvenile pines (cf. *w*, figs. 9 and 10); fig. 15, course of vascular bundles in shoot of juvenile pine bearing juvenile leaves: c^1, cauline vascular bundles; f^1, foliar vascular bundles; *x*, xylem; *p*, phloem; fig. 16, course of vascular bundles in proliferating spur shoot: xylem inside (crossed lines), phloem outside, and cambium between, also resin canals and medullary rays; f^1, foliar bundle consisting of 2 semi-bundles each divided by well defined medullary rays; fig. 17, part of foliar bundle (f^1) in needle of proliferating spur shoot (collected May 3, 1918), part of f^1 of fig. 16: *c*, cambium active and producing spring wood above (*x*) and phloem (*p*) below; l^1, wood vessels; m^1, medullary rays; note that revegetation begins sooner in proliferating shoots than in normal spur shoots, which are still dormant at this season (cf. fig. 1).

may also be derived from juvenile leaves through such transitional forms as bilobed juvenile leaves (figs. 18–20) and concrescent needles[5] (fig. 21).

Histology

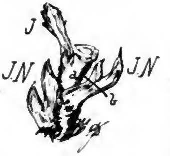

FIG. 18.—Proliferating shoot bearing double (bilobed) juvenile leaves.

The chemical nature of the cell walls may afford good data for the comparison of pine needles with juvenile leaves or with phyllodes of other gymnosperms, living and fossil. Pine needles appear to be more differentiated histologically than morphologically, 18 tissues being recognized from color reactions (see table I).

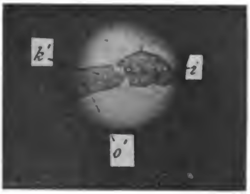

FIG. 19.—Transverse section of double juvenile leaf along plane *ab* of fig. 18; o', double vascular bundles; k', intraparenchymatous resin canals such as usually occur only in needles; *i*, hypodermal resin canal typical of juvenile leaf; microphotograph, obj. 3.

Physiology

Living cells must excrete poisonous materials which result from the disassimilation process (12). In the cells of pines these materials are resinous drops, which must be gotten rid of. In the primitive organs, resin probably filtered through the epidermis, and the epidermal cells were also secreting cells. This is still the

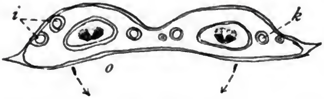

FIG. 20

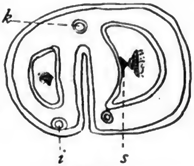

FIG. 21

FIGS. 20–21.—Fig. 20, schematic view of fig. 19: note that each vascular strand contains 2 semi-bundles, as in typical needles; fig. 21, concrescent or double needle: note hypodermal resin canals such as are typical of juvenile leaves, also inverse wood (*s*) on ventral side of protoxylem.

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[5] These concrescent needles have been considered the homologue of the double needles of *Sciadopitys*. They may be homologized with bilobed juvenile leaves bent as shown by arrows in fig. 20.

TABLE I

Histology of adult pine needle	Gentian violet	Methylen blue	Methyl green	Cotton blue*	Sudan III†	Phloroglucin	Devaux's method for pectose‡	Safranin in solution of ferrous chloride	HCl vapors
Cuticle					orange red				
Epidermis: Middle lamella	red	deep blue			orange	red			
Thickening	light violet			green				red	
Hypoderm: Middle lamella	red	deep blue		deep blue		red	blue	red	rose
Thickening	light violet			light blue			blue	red	
Mesophyll								yellow	
Transverse walls of endodermis			deep green			red		red	
Fibers around resin canals							blue		
Periderm		light blue						light rose	rose
Transfusion sheath (inverse wood)					bright orange	light red		red	
Protoxylem (spiral vessels)							blue	rose	
Metaxylem	red	deep blue	green	blue		deep red		deep red	rose
Phloem	violet			blue			blue de Prusse	yellow	
Sclerenchymatous fibers	red								
Cicatricial periderm in cankers					light orange	light red			
Resin drops				blue	orange or yellow				

* Lactophenol solution. † Alcohol and glycerine solution. ‡ Sections stained in ferrous chloride, then washed in distilled water, and treated with ferrocyanide of potassium +HCl; pectose stain "blue de Prusse" (2).

case for the stamens and scales of pines, in which resin is excreted from the epidermal secreting cells. In juvenile leaves most epidermal cells become sclerenchymatous (to protect the parenchyma), and a very few still secrete resin (figs. 22, 23). Internal organs then differentiate, which can store resin, so that parenchymatous cells do not get poisoned, and resin canals run from the needles to the shoot and into the roots. The possibility of getting rid of refuse poisonous material probably explains why coniferous trees are evergreen, whereas most of the other trees periodically lose their leaves and rest in winter.

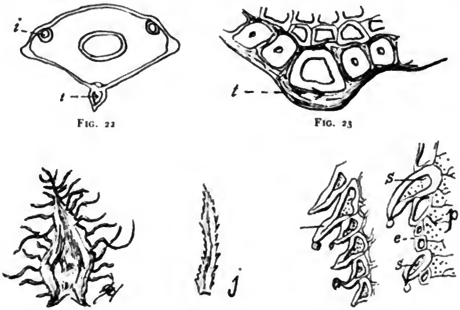

FIG. 22 FIG. 23

FIG. 24 FIG. 25 FIG. 26

FIGS. 22–26.—Fig. 22, abnormal juvenile leaf showing secretory hair (*t*) on ventral face; fig. 23, abnormal needles showing rudimentary secretory hair (*t*) on ventral face; fig 24, scale leaf: strikingly similar to scale of *Cycas;* the hairs may be interpreted as sterilized ancestral ovules or stamens: fig. 25, juvenile leaf, showing hairs that may be interpreted as ancestral stamens, now sterile and secretory; fig. 26, secretory hairs of scale leaf (left) and juvenile leaf (right): *s*, secretory hair; *e*, epidermal cell.

Pathology

The needles of *Pinus maritima* may last 5 or 6 years. Often their death must be due to an accident, either a general trouble in the nutrition of the tree, or a local infection by rust or smut.

In the piñadas of Gascony, many of the needles which are infected in early spring by the aecidium of *Coloesporium senecionis* (*Peridermium oblongisporum* Kleb.) dry up and fall in summer. The "maladie du rouge" is very prevalent and the most important cause of the falling of needles, bringing ruin to many pine nurseries. It derives its name from the red patches that appear and spread on infected needles. It is due to several species of Ascomycetes: *Lophodermium pinastri*, which is the most common on several species of pine (*P. sylvestris*, *P. Pinea*, *P. maritima*); *Hypoderma pinastri*, the conidial form of which was observed by DUFRENOY on *P. maritima;* and *H. strobicola*, observed by FRON on *P. Strobus.*

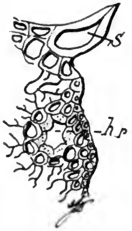

FIG. 27

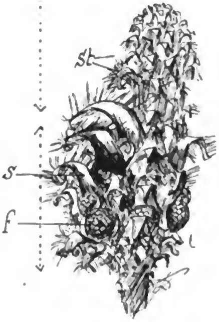

FIG. 28

FIGS. 27–28.—Fig. 27, transverse section of juvenile leaf: *s*, secretory hair; *hr*, hypodermal resin canal; fig. 28, staminate cone of *P. maritima:* basal part, protected from sea wind by ridge in dune, normal and fertile (*s*, scale; *f*, flowers); upper part, exposed to sea wind, sterilized; collected on sand dunes of Arcachon, May 1917; note gradual reduction and sterilization of flowers from base upward.

Conclusion

Morphological variations are but the result of physiological variations (**9**). The different forms of the different phyllodes of pines, juvenile leaves, scale leaves, fertile leaves (♂ and ♀ flowers), and assimilatory organs (needles) differ widely; but abnormal transitory forms (figs. 24–28) which we have observed and described in previous works (**9**) allow us to state that all the forms of the different organs of pines are but different distorted features of a unique ancestral organ which, like the gametophyte of ferns, possessed at the same time the three different physiological functions of reproduction, assimilation, and protection (**10, 11**).

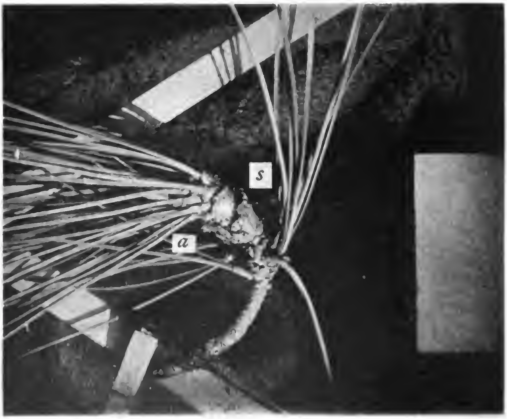

FIG. 29.—Photograph of ♂ inflorescence of *P. maritima*, shoot bent by sea wind; *s*, sterile scales on upper exposed side, with rudimentary ♀ flowers developing at base of scale in place of normal ♂ flowers; *a*, normal ♂ flowers on protected side; sterilization is gradual from protected to exposed flowers.

All the phyllodes of the primitive coniferous trees were probably fertile, and like the fertile leaf in *Cycas*, but under the pressure of unfavorable ecological conditions some parts became sterile scales. This is not mere formal hypothesis; such a sterilization has actually been observed. On the dunes of Gascony, for instance, the parts of the male flowers which are exposed to sea wind are sterilized (fig. 29), and scales develop in the place of stamens (**8**).

In like manner all the different organs must have descended from the ancestral organ; each lost the possibilities corresponding to the function it lost, but retained and perfected those which made it more adequately adapted to its special function. The following table shows how the different organs of pines may be derived from one another, according to data given by studies of abnormal, intermediate forms at the Biological Station of Arcachon.

- Primitive organ
  - fertile (reproduction)
    - ♂ fertile leaf
    - ♀ fertile leaf
  - green (assimilation) → juvenile leaf
    - shoot
    - needle
  - storage of reserves → cotyledonary needle (**7**)
  - self-protecting → scale

A needle which has specialized in the assimilation of carbon is itself a sort of assimilating organ; leaves of angiosperms are another.

Needles are the physiological leaves of pines. They differ from leaves in that they are perennial and are much less fragile. Typical leaves are temporary, delicate, perfectly shaped for intense assimilation, but unable to stand bad weather. Pine needles last several seasons. They have efficient xerophytic adaptation and can stand the roughest weather on arid lands, windy mountain tops, or storm beaten coasts (**15, 16, 17**).

In conclusion, thanks are extended to Professor **Fron** for his valuable encouragement, and to Dr. F. **Lalesque**, Honorary President of the Station Biologique d'Arcachon, for his many kindnesses and valuable documents.[9]

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[9] We are also indebted to The Bureau of Plant Industry, Professor R. T. **Baker**, Dr. **Fragoso**, and Professors **Guilliermond** and **Maire** for most valuable papers; while part of the expenses involved in these researches was defrayed by a grant from the Association Francaise pour l'Avancement des Sciences.

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BRIEFER ARTICLES

JOSEPH YOUNG BERGEN

(WITH PORTRAIT)

There are many ways of advancing science, and hardly less significant than the investigator is he who makes men wish to investigate. Unquestionably no small number of those who have advanced botany have come to it with an inclination formed before university days, and he who set their compass was often one of those wise enthusiasts who guided their first steps in science.

If we should take into account this service alone, American botany would acknowledge its debt to JOSEPH YOUNG BERGEN, who died at his home in Cambridge, Massachusetts, on October 10, 1917. He was born February 22, 1851, at Rye Beach, Maine, his family moving in 1855 to Peoria, Illinois, where for some years the family home was beautifully situated on the bluffs outside the city. Here the nature-loving parents were accustomed to take their children on pleasant country trips to gather flowers, fruits, or nuts, according to the season. This home influence was strengthened for our future botanist by an intimate acquaintance with Dr. STEWARD, an old-time physician of Peoria, who took the lad on many of his professional drives into the surrounding country. This amateur botanist watched the progress of growing things along the roadside, and new or especially interesting plants found their way into the doctor's buggy for more careful inspection at his leisure.

Although the boy was prepared for college chiefly by home study, he had some time in the grammar and high schools in Peoria and two years in the old academy at Pembroke, New Hampshire. In due course he went to Antioch College in southern Ohio, that small but memorable institution whose first president was HORACE MANN, of well known influence in the educational world. It is probable that at Antioch he received that bent toward geology which led to his first scientific work, done in connection with the Ohio State Geological Survey. Later he made practical application of his geological and chemical training in dealing with the problems of lead and zinc mining at Joplin, Missouri.

In 1876 he married FANNY DICKERSON, also of Antioch College, in collaboration with whom in 1890 he published "A Primer of Darwinism and Organic Evolution." Mrs. BERGEN's interests turned later to American folk lore, to which she has made a significant contribution.

In 1878, not long after his marriage, Mr. BERGEN returned to New England and began his long career as a teacher by becoming principal of the high school at Deerfield, Massachusetts. Three years later he accepted an appointment as professor of the physical and biological sciences at Lombard College, a position which he relinquished after 2 years. In 1887 he became teacher of physics in the Boston Latin school. Physics as taught in the high schools of the time was more often an exercise in textbook study than one of application of principles to laboratory practice. Doubtless to one of Mr. BERGEN's broad experience and keen perception of real values the lack of adequate presentation came home with unusual force. In 1891, in collaboration with Professor E. M. HALL of Harvard University, Mr. BERGEN brought out the well known textbook in high school physics which had a far-reaching and permanent influence on the teaching of this science in America. Although his chief interest was later transferred to botany, he maintained an active connection with the teaching of physics by acting for 10 years as instructor in this branch in the Harvard summer school.

In 1889 Mr. BERGEN went to the Boston English high school as a teacher in biology, where he remained for 12 years, during the remainder of his career as a teacher. Here again the need of a new presentation of his subject for high school work led to the writing of his "Elements of Botany" in 1896. The practicable way in which the main features of the newer botany with its greater emphasis on the physiological aspects of the subject were brought out in text instruction and directions for laboratory study went far to make the book an important influence in turning botanical instruction in secondary schools away from the rather dry descriptions of form, to the more interesting and equally valuable study of the activities of life. This book and its successors, the "Foundations of Botany" (1901) with keys to the commoner plants of the great divisions of the country prepared by Miss ALICE EASTWOOD, Professor S. M. TRACY, and by himself, the "Principles of Botany" written in collaboration with Dr. BRADLEY M. DAVIS in 1906, "Essentials of Botany" (1908), "Practical Botany" in collaboration with Dr. OTIS W. CALDWELL in 1911, and "Introduction to Botany" by the same authors in 1914, have provided a series of elementary texts which have kept abreast of the newer movements in botanical development and have served to induct a vast host of young Americans into the study of plants. The success of these books brings sufficient evidence of a wise choice of material and of clearness and adequacy of presentation.

While MR. BERGEN is perhaps most widely known as a teacher and writer of books, he was also a genuine investigator. Both by early training and by inclination a man of out-of-doors, he found his instincts for the field leading him toward the problems of ecology, and his perhaps equally strong inclination toward the precision of the laboratory investigator led him when opportunity presented itself to a fruitful application of laboratory methods to the study of plants in their environment. His opportunity came when in 1901 he retired from teaching and went to southern Italy, where in the neighborhood of Naples he spent some 4 years. Here he made use of the rich facilities of the Biological Station and made the valued acquaintance of FEDERICO DELPINO, Professor of Botany at Naples University, and of other members of the botanical faculty. He found great delight in tramping with Professor MATTEI, now of Palermo, who at that time was mapping the flora on the Solfatara, the partially active volcano near Pozzuoli. After a midday dinner at the Bergen residence they would "tramp off over that wonderful phlegrain plain, perhaps through a basaltic paved Greek lane, perhaps passing some wonderful ruined Greek temple or haunt of Horace or Virgil on their way out into the country." The results of this happy time found their way to the botanical world chiefly through short articles printed in the BOTANICAL GAZETTE and in *Plant*

World between 1903 and 1909. The transpiration problems of the xerophytes of the Neapolitan region, drought tolerance, reactions to light, and the behavior of strand halophytes were among the subjects dealt with in at least a dozen articles. One article on his friend DELPINO (Science **21**:996) recalls the personal relations of those days.

Of course to one whose life had been given largely to teaching, pedagogical matters would necessarily present their claim, and here Mr. BERGEN's broad experience and sympathetic common sense always contributed genuine substance to the discussion. After his return to Cambridge from Italy, Mr. BERGEN's time was for the most part spent on his series of textbooks.

Although Mr. BERGEN took but little part in the work of scientific societies, the circle of botanists and zoölogists who in their Cambridge days found the Bergen home a place of sincere hospitality and of helpful appreciation and encouragement would of itself form a very respectable society. The direct searching comment, the enthusiastic cheering-on, and the sympathetic and straightforward honesty met there were tonic and corrective and stimulant all in one. There are many of us who feel that we owe him a never-to-be-forgotten debt for these and for still more precious gifts.

I am permitted to add an incident told immediately after Mr. BERGEN's death by the gentleman to whom it happened. A few years ago a western botanist, visiting the Harvard Botanic Garden, noticed a tall, spare man of distinguished appearance deeply absorbed in some observations he was making among the flower beds. The visitor asked one of the old gardeners near by if he could tell him the gentleman's name. The old man replied "We call him Saint Joseph."

I believe that in every one of the wide circle of those who called Mr. BERGEN friend this incident will find an echo. In remembering him we value the botanist and the teacher, we respect the far-reaching penetration and creative work of the scientist, and we acknowledge and revere the rigor, the force and moral fervor, the patience and exceeding gentleness of the saint.—RODNEY H. TRUE, *Bureau of Plant Industry, Washington, D.C.*

CURRENT LITERATURE

NOTES FOR STUDENTS

Development in gymnocarpous Agaricaceae.—In a recent paper Miss Douglas[1] describes the development of 7 species of gymnocarpous Agaricaceae. She studied one species of *Mycena* (*M. subalcalina*), 3 of *Hygrophorus* (*H. miniatus*, *H. nitidus*, and *H. borealis*), and 3 of *Entoloma* (*E. flavifolium*, *E. grayanum*, and *E. cuspidatum*). The general course of development is alike in all the species, the variations presented relating to specific or generic features. The fundament of the fruit body just before the differentiation of the stipe and pileus primordia is cone-shaped, homogeneous in structure, the hyphae more or less interlaced and branched, extending in general parallel with the central axis of the cone. The surface is more or less floccose from the ends of single hyphae, or minute tufts, which diverge slightly. The young fundament of *Entoloma cuspidatum* differs from that of the others in being greatly elongated in proportion to its diameter, being nearly cylindrical, or even slightly clavate, with a conoid apex. The slender, elongate fundament appears to bear a direct relation to the slender form of the mature basidiocarp, and also to the very moist habitat of the species. The specimens studied were growing in sphagnum. The rapid elongation of the fundament serves to bring the growing points out of the watery environment in which they originate at the apex of slender rhizomorphs.

The growing point for the formation of new tissue is apical, while elongation occurs in the older hyphae. The first evidence of pileus formation is a great increase in the apical hyphae which begin to diverge, thus giving to the young fundament a sheaflike form. The pileus and stipe fundaments are thus differentiated. While apical growth of the basidiocarp continues, the most active seat of new tissue formation is now shifted from the apex to the annual furrow between pileus and stem primordia, and later to the under surface and extreme margin of the pileus. This marks the origin of the hymenophore. It begins at once in the 3 species of *Hygrophorus*, but is delayed for a short time after differentiation of the stipe and pileus fundaments in *Mycena subalcalina* and in the 3 species of *Entoloma*. It is recognized by the rich protoplasmic content of the hyphae, which usually react more strongly to stains, and thus become more deeply colored. The growth direction of these hyphae of the hymenophore primordium is perpendicular to the point of their origin, whether over the upper end of the stem, in the angle between stem and pileus, or on the undersurface of the pileus. Their course is parallel, although in the angle of the furrow there is more or less of a convergence in their growth direction. At first these hyphae are very slender and terete, but later they become stouter and blunt. From the time of their origin they form a palisade layer whose surface is, in general, level until gill formation begins. In the majority of the species, the ends of the hyphae soon reach the same level. Their "register" is even, and the surface compact; but in *Hygrophorus miniatus* and *H. nitidus* the palisade for some time is not compact and the hyphae do not register evenly. The even register of the palisade hyphae is delayed in these species for some time after the origin of the gill salients.

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[1] Douglas, Gertrude E., The development of some exogenous species of agarics. Amer. Jour. Bot. 5:36–54. *pls. 1–7.* 1918.

During the early stages of development of the hymenophore there is a strong epinastic growth of the pileus margin, causing it to curve downward and inward. This is particularly strong in most of the species, less so in *Entoloma cuspidatum* and less so in *Hygrophorus nitidus*. The gill salients are formed by the more rapid downward growth and extension of the subjacent tissue in regularly spaced radial areas. The development advances in a peripheral direction from the stem toward the margin of the pileus. The growth direction is perpendicular to the morphological undersurface of the pileus, and the situation from this standpoint can readily be understood when the pileus margin is strongly incurved.

In the palisade layer, which eventually becomes the hymenium, the elements are multiplied by branching of the subhymenial elements. In the species of *Hygrophorus* in particular, and to some extent also in *Entoloma flavifolium*, the pressure of the increasing palisade loosens up the elements of the subhymenium, and this is evident as a zone of less density. This peculiarity is well shown also in *Omphalia chrysophylla* and *Clitocybe cerussata* studied by BLIZZARD.[2]

In both these papers dealing with gymnocarpous forms, it is shown that the origin and the general course of development of the hymenophore corresponds with that of angiocarpous forms of the *Agaricus* type. It is further shown that there is a tendency in the early stages of development for a superficial zone of the pileus, here of quite limited extent, to be arrested in growth, sometimes quite regularly and normally. The regular course of development being thus shifted to a slightly interior zone presages the later evolutionary type of development presented by the angiocarpous forms, where the origin and differentiation of stipe and pileus primordia are shifted permanently to the interior of the young basidiocarp primordium, with a more or less well marked external zone, the blematogen.—GEO. F. ATKINSON.

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[2] BLIZZARD, A. W., The development of some species of agarics. Amer. Jour. Bot. 4:221–240. *pls. 6–11.* 1917.

Self-sterility.—EAST and PARK[3] have recently published the results of some extensive experiments on 4 self-sterile species of *Nicotiana*, and have proposed an explanation. In the past there have been several attempts to interpret self-sterility as a response to environmental factors, notably humidity. Such interpretations may have been quite true in some cases of self-sterility, where only a single race of plants has been involved, but highly unsatisfactory in explaining cases where pollen fails on own stigmas and functions on stigmas of another race. It is such a situation that the authors have dealt with, and they have shown conclusively for their material that self-sterility is inherited. Normal seasonal changes at times induced "pseudo self-fertility" in their self-sterile races, but "other environmental factors appeared to have little or no influence on self-fertility."

As to the physiological nature of self-sterility, the authors state that it is involved with rate of pollen tube growth. This in itself suggests that self-sterility behaves as a sporophytic character. The fact is more definitely demonstrated, however, "by the behavior of reciprocal matings, pairs of reciprocals always giving like results either when fertile or sterile."

Going further, the authors state "that modern discoveries tend more and more to show that the sole function of the gametophyte of the angiosperms is to produce sporophytes. The characters which they possess appear to be wholly sporophytic, the factors which they carry functioning only *after* fertilization." This statement seems directed at such theories as that of BELLING, who has given us a striking explanation of "semi-sterility" in beans, on the basis of the direct influence of the germinal equipment of gametophytes upon the gametophytes themselves. It is quite probable, however, that the two cases are involved with distinctly different phenomena, since BELLING'S material showed degeneration and sometimes complete abortion in pollen and embryo sacs, while the Nicotianas of EAST and PARK were self-sterile merely because of the failure of pollen tubes. The hereditary mechanism of the two cases must be quite different.

To explain the hereditary behavior of their Nicotianas, the authors have assumed a mechanism involving multiple allelomorphs and crossing over. If two plants differ in but one of a number of effective factors, they are fertile in intercrosses. "Intrasterile classes" are composed of individuals which differ in none of the effective factors. Anything like a thorough appreciation of this theory can be obtained only from the original article.

This explanation seems sufficiently accurate in interpreting the results of the authors, as well as the results of some of the earlier investigators. From a practical point of view, however, it seems rather unsatisfactory, since it considers only the behavior of self-sterile plants when bred *inter se*. The authors state that "all questions connected with the relation between true self-fertility and self-sterility have been omitted designedly as pertaining to a distinct problem." Are we unreasonable in asking for a single theory to explain both self-fertility and self-sterility? Are we wrong in thinking that the significance of self-sterility lies in its relation to self-fertility? Such a general theory, no doubt, will be provided by the authors in their later reports; the present publication evidently represents merely the first of a series on the general subject of self-sterility.

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[3] EAST, E. M., and PARK, J. B., Studies on self-sterility. I. The behavior of self-sterile plants. Genetics 2:525–609. 1917.

The explanation also has another theoretical shortcoming, similar to that which applied to EAST's "heterozygosis." In heterozygosis EAST stated that hybrids are vigorous because of their heterozygous sets. This virtually amounted to saying that hybrids are vigorous because they are hybrids. "Heterozygosis" was a more accurate and scientific statement of the fact of hybrid vigor, but it was not an explanation. Now EAST states that pollen will not function on stigmas of a plant of which the germinal constitution is the same as that of the plant which produced the pollen. Couched in a terminology involving multiple allelomorphs and crossing over, this may well be a more accurate and scientific statement of the facts of self-sterility and its behavior in inheritance, but it is not an explanation. Such scientific restatements are very valuable in helping to organize facts, and "heterozygosis" unquestionably had such a value. The present theory, however, seems at first sight a much less valuable one, since it is so elastic as to be confusing.

But whether the theoretical argument of the authors is destined to stand or fall, they have done an exemplary piece of research. This seems to have been the first satisfactory experimental attack upon the problem of self-sterility, and the resulting data are therefore extremely valuable.—MERLE C. COULTER.

Buffer processes in succulents.—JENNY HEMPEL[4] has made a very important addition to our rather limited knowledge of actual reaction in plants. Succulents were used in this work, since, with their well known wide and rapid variations in acid content, they might be expected to supply especially interesting material for such a study. Determinations by the use of the hydrogen electrode were made on the juices of numerous specimens of the plants studied, after they had been exposed to varying conditions. The values found range from $P_H = 3.9$ to $P_H = 5.7$. Higher acidity than the more acid of these values is recorded in the same work in lemon juice ($P_H = 2.19$); and by HAAS[5] in citrus fruits ($P_H = 2.22$–3.8), in cranberries ($P_H = 2.4$), and by a less exact method[6] in the petals of certain flowers ($P_H =$ about 3).

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[4] HEMPEL, JENNY, Buffer processes in the metabolism of succulent plants. Compt. Rend. Trav. Lab. Carlsberg **13**:1–129. 1917.

[5] HAAS, A. R. The reaction of plant protoplasm. BOT. GAZ. **63**:232–235. 1917.

[6] ———, The acidity of plant cells as shown by natural indicators. Jour. Biol. Chem. **27**:233–241. 1916.

It would seem that such marked changes as were found in the reaction of the juices of active tissue must affect considerably the metabolic processes, as well as the physical condition of the tissue. CROCKER[7] has suggested that these changes may be important in the regulation of transpiration by succulents. The lower values are of the same order as those reported in the same work by HEMPEL and also quoted from WAGNER for non-succulent plants. Such P_H values range from 5.4 to somewhat above 6. Slightly alkaline juices are reported by HAAS (*loc cit.*) in the petals of certain flowers; he finds, however, that blue pigments by no means always indicate an alkaline reaction.

As the title suggests, the principal object of the work was to gain some information as to the substances in the plant juices which act as buffers, or regulators of their reaction. On the acid side of the neutral point the following data were obtained for this study: (1) titration to the litmus end point ($P_H = 6.8$) compared with the original P_H value; (2) qualitative tests to determine the organic and inorganic acid radicals present; (3) ash analyses to determine the total base present; (4) studies of the reaction and titration values of malic acid salts, and such mixtures of them as appear likely to occur in the plant. The data are most complete for the juices of *Rochea falcata*, *Cotyledon obvallata*, and *C. linguaefolia*. The conclusion is reached that in these plants, and probably in all succulents, the concentration of hydrogen ions is determined by the relation between the quantities of acid and normal malate present.

On the alkaline side of the litmus end point the data may be grouped as follows: (1) titration from the litmus end point to that of phenolphthalein (P_H = about 9.2); (2) determination of nitrogen and in some cases phosphorus; (3) titration experiments with aluminum malate; (4) titration experiments with unknown and variable substances precipitated at the phenolphthalein point. It is concluded that aluminum malate and the unknown substances mentioned are the principal buffers in this region. The nitrogen and phosphorous compounds have very little effect. The titration to the phenolphthalein end point is admitted to be very unreliable. It seems unfortunate that as considerable quantities of the juice were available the electrometric method of titration was not used. Such results would have contributed much to the completeness and accuracy of the data.—THOMAS G. PHILLIPS.

Mutationists and selectionists.—JENNINGS[8] has attempted to reconcile the views of the "mutationists" and the "selectionists." The latter, headed by CASTLE, have claimed that selection can modify unit characters, and have presented striking evidence on the point. The mutationists have then demonstrated that these data may also be interpreted by assuming that there is but one basic invariable unit determining the presence or absence of a character, plus numerous modifying factors; the number of the latter present in a given case determines the degree of expression of the character. The author admits that such modifying factors have been demonstrated in *Drosophila*, but goes on to show how "the objections raised by the mutationists to gradual change through selection are breaking down as a result of the thoroughness of the mutationists' own studies." For in *Drosophila* there have gradually been discovered not only 7 modifying factors for eye color, located on different regions of chromatin from the basic factor for eye color, but also 7 grades of the basic factor itself, that is, different conditions of the same unit. "What more does the selectionist want? Is not the controversy at an end?"

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[7] CROCKER, WM., Rev. BOT. GAZ. **64**:526–527. 1917.

[8] JENNINGS, H. S., Modifying factors and multiple allelomorphs in relation to the results of selection. Amer. Nat. **51**:301–306. 1917.

———, Observed changes in hereditary characters in relation to evolution. Jour. Wash. Acad. Sci. **7**:281–301. 1917.

There still remains, however, a fundamental difference between the two views. The selectionists claim that these changes (in unit characters) are continuous, and in a definite direction determined by the standard of selection. The mutationists, on the contrary, claim that these changes occur in distinct steps (mutations), and do not occur in any definite order or direction as the result of selection. JENNINGS takes exception to this last claim of the mutationists, and presents some of his work on protozoa, to show the effectiveness of selection in a series of asexual generations.

There is much to be desired in such a reconciliation between the two schools, but more evidence must come in before there can be much hope of bringing it about. At present the views of the mutationists seem to be in better favor, chiefly because they give a much more definite basis for description of the phenomena of inheritance. "If one creates a hypothetical unit by which to describe phenomena and this unit varies, he really has no basis for description (EAST)."—MERLE C. COULTER.

Narcotic plants and stimulants.—SAFFORD[9] has published a very instructive account of plants used by the "ancient Americans" as sources of narcotics and stimulants long before the discovery of America. He indicates 13 such plants as chiefly in use, among them *Nicotiana, Datura Stramonium* (a source of atropine), *Erythroxylon Coca* (a source of cocaine). Other plants of minor importance are also noted. In concluding the summary, the following statement is made: "In view of the shortage of medicinal alkaloids resulting from the present war, it is suggested that investigations be made to determine the nature of the properties of these less-known narcotics, with a view to their utilization as substitutes for others now recognized in the standard pharmacopoeias."—J .M. C.

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[9] SAFFORD, W. E., Narcotic plants and stimulants of the ancient Americans. Smithson. Rep. 1916. pp. 387-424. *pls. 17.* 1917.

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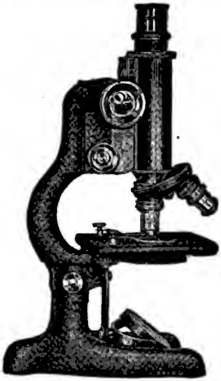

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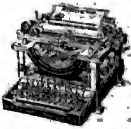

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THE
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LIMITING FACTORS IN RELATION TO SPECIFIC RANGES OF TOLERANCE OF FOREST TREES

A. H. HUTCHINSON

(WITH SEVEN FIGURES)

The conclusions recorded in this paper are drawn from a study of the forests throughout the Province of Ontario, particularly along the shores of Lake Ontario, Lake Simcoe, the Kawartha Lakes, and Rideau Lakes; in Algonquin Park and in Mattagami and Timagami Forest Reserves. Observations, with notes, have been made during more than 6000 miles of travel by canoe and overland through the forest country of northern Ontario, especially along the streams and lakes forming the headwaters of the Muskoka, Maganatawan, Petewawa, and Madawaska rivers; also of the Montreal, Sturgeon, Wanapitei, Vermilion, Mattagami, and Abitibi rivers. While the greater part of the discussion has particular reference to Ontario, the conclusions are made in the light of some personal knowledge of the forests southward to the Gulf of Mexico and westward to the Pacific.

The data regarding the limits of forest trees recorded in the accompanying maps have been obtained principally from accounts of the explorations of BELL (**2**), MACOUN (**19, 20**), and LOW (**18**). The records of isotherms and precipitation areas have been copied from the Geological Atlas of Canada, 1915. So far as the writer has been able to observe, the records of the explorers mentioned have been even more accurate than has generally been conceded. Although the specific limits of forest species have been rather definitely outlined, there seems to be no agreement regarding the part played in determining these limits by the various factors affecting forest growth. In this paper an attempt has been made to relate the limiting factors to the specific range of tolerance of forest trees, and in this way to account for the respective distributions of some of the species dominating the forests of Ontario.

SCHIMPER (21), as a result of his extensive studies in plant geography, concludes that "the differentiation of the earth's vegetation is thus controlled by 3 factors: heat, atmospheric precipitation (including winds), soil. Heat determines the flora, climatic humidity the vegetation; the soil as a rule merely picks out and blends the materials supplied by these two climatic factors, and on its own account adds a few details."

Investigators have mentioned many factors which affect the composition of forests. Drawing his conclusions from the exploration of Labrador, LOW (18) says "the distribution of forest areas and the range of the various trees depend upon several factors, among which may be mentioned position as regards latitude, height above the sea coast, and the character of the soil." BOWMAN (3) in the light of his physiographic studies says as follows:

> The distribution of forests is controlled largely by rainfall, although the distribution of species within each region is also controlled by insolation, temperature, wind velocity, water supply, and geographic relation to post-glacial centers of distribution. When more detailed statements are attempted many difficulties are encountered in the form of apparent inconsistencies. Some species appear to find their appropriate conditions in different latitudes by a change in their habitat; for example, the larch, balsam fir, and white birch which in the north grow freely on dry or hilly ground, toward the southern limits seek the cold ground in swamps. The white cedar and white pine in some places manifest the same tendency.

FROTHINGHAM (12) in his report on hardwood forests sums up the situation as follows: "How moisture and temperature affect the different species in the complexity of forest environment is still so little known that no positive information can be given."

Temperature factor

The northern limits of many tree species are undoubtedly the result of low temperatures. WARMING (24) states, "It is clear that conditions as regards heat determine the boundaries of the distribution of species on the earth." The effect of temperature is emphasized by the fact that "the appropriate temperature for the growth of a number of species, such as *Picea* and *Abies*, is carried far to the south of their normal latitudes along the elevated parts of the continent, especially the Alleghanies and Rocky Mountains" (BELL 2). In such regions the tree species are in most cases identical with those found farther north. However, it is more difficult to account for the southern limits of trees on a basis of minimum temperature. BRAY (5) finds difficulty in explaining the occurrence of boreal (*Picea*, *Abies*) associations in the bogs of regions dominantly austral. "The question arises as to whether the factor of temperature plays a rôle in the occurrence of these bogs," and again, "the extremely irregular boundary between the boreal conifer forests and the temperate hardwood forests of New England, for example, can hardly be explained by temperature alone" (HARPER 14).

The lines representing the limits of *Picea nigra*, *Larix americana*, and *Betula papyrifera* follow yearly isotherms very closely from the mouth of the Mackenzie River across the continent until they reach the coast of Labrador, where they swing southward, here following a course almost parallel with the coast line. There is reason to believe that temperature is the limiting factor throughout a great area, while a second factor is active along the Labrador coast. From the fact that the same order in the limitation of these species is retained, even in the Labrador region, it would seem that the limiting factors are similar throughout. Excessive loss of heat energy due to the air currents so prevalent in this region has the same effect as the loss of heat energy due to excessively low temperatures. Similarly in southern Ontario, where latitude and lake influence together result in a region of a relatively high yearly temperature average, the limits of trees such as *Juglans nigra* and *Castanea dentata* are parallel with isotherms. Here also the evidence would indicate that temperature is the limiting factor with respect to such species. The general conclusion that temperature is usually, if not universally, the determinant of northern limits has resulted from making general statements based upon selected and favorable instances which are specific rather than general.

There is abundant evidence that while temperature acts as a limiting factor in many instances, it is by no means the only factor controlling even the northern limits of tree species. This is amply demonstrated by the data recorded on the accompanying map (fig. 1). Many of the lines indicating the northern limits of tree species intersect; this cannot be accounted for on a temperature basis. Isotherms do not intersect nor do lines indicating the length of the growing season. The northern limit of ***Pinus Banksiana*** at 100° W. long. traverses a region the yearly isotherm of which is 25° F.; at 80° W. long. the isotherm which the northern limit traverses is 32.5° F.; at 75° W. long. it is 20° F.; and at 70° W. long. it reaches the 32.5° F. isotherm. The isotherms corresponding to the northern limits of ***Ulmus americana*** at various regions are at 100° W. long. 27.5° F.; at 95° W. long. 32.5° F.; at 80° W. long. 30° F.; at 75° W. long. 40° F.; and at 70° W. long. 32.5° F., a remarkable range of variation. The looping of the lines representing the limits of such species as ***Picea canadensis***, ***Populus balsamifera***, and ***Populus tremuloides***, as shown in the Labrador region (northern Quebec), is significant, particularly in the case of ***Picea canadensis***, in contrast with the closely related ***Picea mariana***. The northward deviation of the limits for ***Betula lutea***, ***Acer saccharum***, ***Tsuga canadensis***, and ***Quercus rubra*** at 80° W. long., a point where the isotherm swings southward, cannot be explained on a temperature basis. The anomalous tree distribution in the Saugenay region is another case in point. Any idea of the possibility of explaining the western limits on a temperature basis has long been discarded. It is evident that in the instances mentioned something other than temperature must be the limiting factor.

Water factor

Water as a factor in the determination of tree distribution has received considerable recognition. COWLES (**8**) says, "On the whole there has been a general tendency to overestimate the influence of

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temperature as an ecological factor. The trend of nearly all experiment has been to show that water is of vastly greater importance." BELL (2) states, "A great difference in the moisture of the air of two regions otherwise resembling each other in climatic conditions has also a powerful effect upon the growth of forests; and the dryness of the air in the western prairie and arid regions is, no doubt, the chief cause of the absence of timber."

There has been much recent research concerned with the water relation of plants (**9**). The greater number of investigators have selected the region of the great plains, a region where water is dominantly the limiting factor, as their field of investigation. TRANSEAU (**22, 23**), LIVINGSTON (**16, 17**), and FULLER (**13**) have shown that the water factor may be regarded as a complex depending primarily upon the amount of soil water available for the plant and the rate of evaporation. The amount of available soil water is dependent upon precipitation during the growing season and the physical properties of the soil, while evaporation depends chiefly upon the humidity, air currents, and temperature of the atmosphere. BRIGGS and SHANTZ (**4**) in their work on the wilting coefficient have emphasized the specificity of tolerance in plants with respect to minimum soil water. The valuable experimental data recorded in these papers demonstrate that water frequently acts as a limiting factor; the converse, that there is a considerable range for any given species wherein water does not factor in a limiting capacity, is less frequently emphasized.

It is significant that the limits of tree species such as *Picea mariana*, *P. canadensis*, *Larix americana*, *Populus balsamifera*, *Abies canadensis*, and *Betula papyrifera*, which extend north of the arid plains, are not deflected southward in the Manitoba-Minnesota region, while almost invariably the more southern species are deflected when they come in contact with the region of diminished precipitation. The evidence would indicate that the water factor limits the westward extension of such species as *Acer saccharum*, *Tsuga canadensis*, *Fagus americana*, *Thuja occidentalis*, and *Ulmus americana*.

It may be noted, also, that when this deflection takes place the order in which the tree limits occur is changed in many instances.

Thuja occidentalis, which extends northward far beyond *Acer saccharum*, does not reach the western limits of the latter, while *Quercus rubra* extends westward beyond the limits of many species which are to be found beyond its northern limit. Such phenomena doubtless are the result of the fact that different limiting factors dominate the several regions forming the boundaries of distribution.

In southeastern Canada it is difficult to find any parallelism between the limits of tree species and the boundaries of precipitation areas. For instance, *Juglans cinerea* extends throughout areas whose respective yearly precipitations are 30–35 in., 35–40 in., 30–35 in., 40–45 in., and 45–50 in., with no apparent deflection of the lines bounding its growth area. The limits of *Fagus americana* pass through similar areas, with the addition of an area where the minimum yearly precipitation is 25 in. This range is of particular significance in consideration of the fact that *Fagus* is generally regarded as mesophytic. The absence of a parallelism between precipitation and forest limits in the Ontario section is so obvious from a consideration of the accompanying map (fig. 2) that further emphasis would be superfluous. Other conditions being favorable, there is sufficient rainfall for forest growth; or, in other words, precipitation does not enter here as a limiting factor.

WARMING (**24**) has based his ecological classification of plants upon the premise that "the most potent and decisive factor is the amount of water in the soil." "The soil upon which the coniferous forest occurs varies widely, yet so far as reliable information is available it is always physically or physiologically dry." "The cold winter is a physiologically dry season against which trees can protect themselves by defoliation or by xerophytic structure." This may account for the xerophytic structure of the coniferous leaf; it is difficult to understand what bearing it has in connection with the contention that conifers as a class grow in dry soil conditions, the winter, even for conifers, being a period of comparative dormancy. Deciduous trees are protected against the "physiological dryness" of winter by leaf fall; conifers by having leaves of xerophytic structure. Some deciduous trees, for example *Quercus*, are comparatively xerophytic, while others are decidedly meso-

in i

phytic, as *Fagus* and *Acer*. It seems possible that there might be a similar range amongst conifers. Zon (27) states, "Balsam fir attains its best growth and largest size on flats the soil of which is usually a moist, deep sand-loam." An abundance of available soil water is not the factor which so often excludes *Abies balsamea* from such soils, particularly in the more temperate regions.

During the summer of 1914 a series of experiments were conducted in Algonquin Park to discover the relation of seedling growth to atmospheric humidity. Atmometers of the Livingston design were set up at a number of stations, including those where seedlings of *Acer saccharum*, *Abies balsamea*, and *Picea mariana* were abundant. The readings for the months of July, August, and part of September proved that in this region there is no appreciable difference in the rates of evaporation at the stations mentioned, and that in each case the humidity was in excess of that which Fuller (13) regards as characteristic of a mesophytic forest. Moreover, *Acer* grows on the more exposed ridges; *Abies* and *Picea* on the less exposed lowlands or slopes. Experiment has shown that such conditions hold generally for the "lake country," where in many cases one-tenth of the total area is covered by water, and the greatest distance of any point from bodies of water seldom exceeds 2 miles. Three of the limiting factors most frequently emphasized, temperature, atmospheric humidity, and precipitation, are eliminated, as such, under conditions prevailing, and still there is a marked segregation of forest associations.

Soil factor

The problem regarding the extent to which soil composition may act as a limiting factor in the determination of forest distribution has been variously answered. Frothingham (12) states "The soils of the northern hardwood forest are as a rule loamy sands, the results of the decay of granite, quartzites, and siliceous gneisses, also the water assorted loams and clays or the unassorted morainal tills, rich in clay; but they also thrive on light sandy soil in localities subject to moist winds." In connection with the forests of Michigan, Beal and Wheeler (1) state that "The best wheat lands are usually found on uplands near streams, where the oak timber gradually shades into beech and maples." On the other hand, "evergreen trees, whether coniferous or broad-leaved, seem to be just as characteristic of poor soil as of any particular kind of climate" (14). BOWMAN (3) draws attention to the limitations of soil composition as a determining factor. COWLES has shown that the composition of the rock from which any soil may be derived seldom acts in a limiting capacity with respect to the species which that soil may support. It is only in exceptional cases that a soil, newly weathered, is deficient in the mineral constituents necessary for plant growth. This generalization is particularly applicable in Ontario, where the soil, whether it be glacial drift toward the south, or the weathered deposits and exposed rocks farther north, is derived from the dominantly granitic rock of the Laurentian Plateau. The original composition of the soil is seldom a limiting factor, at least in so far as the forests of Ontario are concerned.

Humus factor

It is scarcely necessary to emphasize the importance of the humus content of the soil as an ecological factor; its significance as a limiting factor with respect to the forests of Ontario is our chief concern. In forest regions the humus content of the soil increases the water retaining capacity; increases the porosity, and hence the aeration of the soil. Mineral salts are retained by the adsorptive properties of humus, and incidentally, conditions are made more favorable for soil bacteria, which are essential for the growth of such species as *Fagus*. COWLES (8) states, "Although bare sand supports a xerophytic flora, the accumulation of a thin humus layer is sufficient for forest development, and the Michigan dunes show that the most mesophytic of our forests can grow on a sand dune if there is present a humus layer a few centimeters in thickness." In the Algonquin Park region to which reference has been made, the *Acer* or *Acer-Fagus* forest occupies the ridges, while the *Abies-Picea* forest occupies the lower slopes and lowlands. On the slopes where the exposure of the rocks, due to drainage of glacial lakes, has been comparatively recent, only a small amount of rock soil has accumulated; this is covered by a humus layer, but the two are not intimately intermingled by weathering processes. The humus content of the soil proper is low. In the lowlands a similar condition maintains. This is especially applicable to the peat bog, where humus is most abundant. There has been no movement, however, of the particles of the contiguous strata of the rock soil and the overlying humus; they are distinct, hence the otherwise valuable humus is practically useless in so far as the improvement of soil properties is concerned. On the ridges which were exposed first by the subsidence of glacial ice and water there is much deeper soil, and the humus accumulated from antecedent vegetation has become intimately associated with the rock soil by weathering. The soil proper has a high humus content and is able to support such trees as *Acer* and *Fagus*. It will be remembered that the temperature, precipitation, humidity, and original soil composition may be regarded as constant; the varying factors are those associated with the accumulation of humus. The humus content of the soil is at least a local factor in the determination of tree distribution.

It has been maintained that differences in the composition of soil have only a local effect. It does not seem clear why a factor which is potent locally should not be potent throughout greater areas. The gradients of soil changes are usually greater when limited areas are considered; hence also those of the associated floral changes. The Laurentian Plateau is a great area dominated by the coniferous forest, while the contiguous region of glacial drift is dominated by the deciduous hardwood forest. The marked differences in forest species prevailing in the regions north and south of the Kawartha Lakes, respectively, is strikingly in accord with soil differences. Moreover, the line separating the dominantly coniferous region from the dominantly deciduous hardwood region does not follow any isotherm or the boundaries of any precipitation area, but rather the outlines of the Laurentian Plateau, roughly from the southeast part of Georgian Bay to Lake Simcoe along the Kawartha Lakes, southeastward to the Thousand Islands, northward to Ottawa, and again eastward along the northern limits of the Ottawa and St. Lawrence valleys. In the coniferous region there are oases of deciduous hardwoods of considerable area, such as that at Renfrew, or of limited area, such as the ridges already mentioned; in fact, wherever the soil is similar to that found in the characteristically deciduous hardwood area. It is true that these broad outlines have been obscured in many places by large tracts being covered with pioneer forms, such as *Populus* and *Betula*, as a result of "burns" (**10, 11, 15**). These regional forest limitations cannot be explained except upon some basis of soil differences, such as have been described as determining the local limitations of the forest types of Algonquin Park. The evidence clearly indicates that the slowly weathering rock of the Laurentian Plateau has been a barrier against migration of the hardwood forest, which, however, has been able to establish outposts where favorable soil conditions have been found. In brief, the development of a soil, particularly with reference to its humus content, may act as a limiting factor regionally as well as locally.

Light factor

It is generally accepted that seedlings of some tree species grow only where there is abundance of light, while others grow best under shade conditions (**26**). FROTHINGHAM (**12**) has classified the trees of the northern hardwood forest upon the basis of light tolerance. The seedlings of pioneer species are necessarily light tolerant in contrast with those species forming the climax forest, which are shade tolerant; seedlings of *Pinus Banksiana* and *P. Strobus* thrive only in direct sunlight, which is also the case with seedlings of *Abies balsamea* and *Picea canadensis*, although to a less marked degree. On the other hand, the seedlings of *Acer* and *Fagus* grow best in the dense shade of mature trees; *Tsuga canadensis* is an example of a conifer which is similar in this respect. Because of the specificity of the range of tree species with respect to intensity of light, certain forms cannot be pioneers, while others are eliminated from forests which have been well established, except where destructive agencies such as cause windfalls and erosion are at work. To this extent the intensity of light may act as a limiting factor in tree distribution.

Time factor

The time factor deserves a most important place in any consideration of the distribution of forest trees, and it is of particular significance in connection with the forests of Ontario. Time as a factor in limiting the distribution of forest species is an expression of the rate of change in ecological conditions and of the specific rates of migration of the various species. Ordinarily conditions change so slowly that migration keeps pace; when there are more rapid changes migration lags behind. The time factor, therefore, must be considered in relation to the rate of change of such conditions as temperature, water, soil, light intensity, and secondarily in relation to methods of distribution.

WARMING (24) states, "Changes in the physical relationship of the soil are everywhere and always taking place, and in close correlation with this plant communities also undergo modification, but it does not seem possible to use development as the fundamental basis of classification of plant societies." COWLES (7), while recognizing the same factors, attaches more importance to development of successional associations.

The forests of Ontario have been made possible only by the retreat of glacial ice and water and the establishment of conditions permitting the growth of trees. It is evident that modifications of temperature have been prerequisite for the northward migration of tree species; by many it is regarded as the only factor. ADAMS suggests that the northern migration following the retreating glacier would comprise 3 great waves of life: (1) a wave of glacial or arctic vegetation, of which there are remnants in New York and Mount Marcy and two or three other high peaks; (2) a wave comprising the northernmost species of trees, stunted willows, birches, alders, and the coniferous forest spruces, hemlock, and pines; (3) a wave embracing the temperate zone deciduous trees. HARSHBERGER records a similar conclusion: "Several great waves of plant migration may be recognized, namely, glacial vegetation, tundra coniferous forests, and a migration of the deciduous forest elements from the southeastern center." If forest migration has kept pace with temperature changes, it might be expected that the limits of forest species would conform in outline with respective isotherms. It has already been demonstrated that in many instances this is not the case. The conclusion that in many places the migration of such species as *Tsuga canadensis*, *Acer saccharum*, and *Fagus americana* has lagged behind temperature changes is made necessary. To a greater or less extent this is true of all the species forming the forests of Ontario. Under existing temperatures any further migration is dependent upon changes in the conditions now acting as limiting factors, as water, soil, and light. The rate of migration, and hence the distribution of forest trees, is dependent, primarily, upon the rate of change in temperature; however, migration may be restricted by other factors.

There is reason to believe that the yearly precipitation has gradually decreased since the glacial epoch. The data regarding the exact extent of these changes are limited. There can be no doubt, however, that the westward migration made possible by temperature changes has been checked by the water factor; also the irregularity of the limits of *Pinus Banksiana* may be explained by the fact that although temperature conditions have so changed that this species has migrated to 56° N. lat. in the highlands of northern Quebec, it has been limited in its northward progress by the low lying lands south and westward from James Bay. The inconsistencies of data regarding the northward distribution of *Pinus Banksiana* are doubtless due to the presence of certain outliers which might be expected when available soil moisture and other soil conditions act as the limiting factor, but which would be most improbable were temperature the determining factor of distribution. In regions where water is a limiting factor the rate of migration is dependent upon the rate of change in water conditions, in other words, upon the time factor.

Time factor in relation to soil development

It has been demonstrated that soil development, particularly with reference to the humus content, is a potent factor in determining the boundaries separating the *Acer-Fagus* and the *Abies-Picea* forests of Ontario. Since the *Acer-Fagus* forest demands the most highly developed soil, we are forced to the conclusion that in a forest succession the deciduous hardwood forest is the climax type. Over a vast area this climax type of forest has been excluded by soil conditions rather than by temperature. Northward migration of the deciduous hardwood forest has been limited by the rate of soil changes rather than by the rate of temperature changes; with respect to the latter migration has lagged behind. Upon such a basis the "anomalous" separation of the deciduous hardwood forest and the coniferous forest is readily explained. The granitic rock of the Laurentian Plateau has weathered slowly, humus has accumulated slowly; in brief, the soil has developed slowly, hence the migration of the climax forest has been checked. This principle applies regionally as well as locally. In the region of glacial moraines the deep soil has made possible a rapid accumulation of humus, as well as a thorough intermingling of rock soil and humus. There has been a rapid development of the soil, consequently the *Acer-Fagus* forest has been permitted to invade such regions. The time factor as an expression of the rate of soil development has limited the rate of migration and hence forest distribution also.

The time factor in relation to soil development explains both the numerous northerly outliers of *Acer* associations and also the outliers of the *Picea-Abies* forest. The northward deviation of the limits of such species as *Acer saccharum*, *Fagus americana*, and *Tsuga canadensis* has been noted. It is significant that this deviation coincides with a great depression extending to the height of land in which highly developed soil deposits are present. The deciduous hardwoods occur as outliers and are always found on the better soils. Although the writer has not been able to study the Saugenay basin personally, it may be ventured that the northward migration of *Acer* at this point is also to be explained on the basis of soil development. BRAY (5) has found difficulty in explaining the occurrence of such trees as *Abies* and *Picea* in the swamps of New York. The soil in such localities is in a primitive stage of development. Although much humus has accumulated, there has been little or no intermingling of rock soil and humus, and the degree of aeration is low. The soil has been protected from the action of atmospheric agencies and running water, hence its undeveloped condition. The result is the same as when the slowly weathering Laurentian rock resists the agencies which promote soil formation. The fact that the same forest species are present in both places emphasizes the potency of the rate of soil development as a factor in the determination of tree distribution.

The evidence submitted is regarded as sufficient to prove that throughout a great region of Ontario dominated by *Picea* and *Abies* these genera are not permanent or climax forms, since they are replaced by *Acer* when soil conditions become favorable. **Whitford** (**25**), after studying the forests of Michigan, states that soils are improved by coniferous trees, and when sufficient humus soil has accumulated the deciduous species establish themselves. **Bray** (**5**) also implies this relation. **Cooper** (**6**), however, after a study of Isle Royal, comes to the conclusion that "this type (*Abies-Picea-Betula* forest) is the climax forest of that portion of the northeastern conifer region under consideration; in other words, upon Isle Royal it is the final and permanent vegetative stage toward the establishment of which all other plant societies are successive steps. It is the climatic forest of the region, permanent while the climate remains essentially as now." The same paper records stands of *Acer* on certain ridges of Isle Royal and in other places where soil conditions seem particularly favorable. It seems probable that the occurrence of these stands might be explained on the basis of soil development.

It is evident from a study of the forests of northern Ontario that the deciduous hardwood forest is encroaching upon the coniferous forest region, and that the progress of this encroachment has lagged behind temperature changes, being now dependent principally upon the rate of soil development.

The relation of shade to the time factor of distribution is in accord with the specific tolerance of a given species with respect to light. The *Acer-Picea* forest provides shade which is essential for *Acer* seedlings, while detrimental to *Picea* or *Abies* seedlings. The encroachment of the deciduous hardwood forest upon the coniferous forest, made possible by changes in temperature and soil development, is also promoted, and the result made more permanent by decreasing light intensity due to shade conditions.

The importance of methods of seed dispersal as an element of the time factor of distribution is obvious. Where changes in conditions are slow, for instance yearly temperature modifications, even the trees whose methods of dispersal allow them to migrate slowly are able to keep pace, and where ecological changes are more rapid species having the best methods of seed dispersal naturally migrate most rapidly. The rapid invasion of a burned area by the *Populus-Betula* association is due primarily to the widespread dispersal of the seeds of these species. In contrast, *Pinus* takes its place among the trees which appear later, largely because it has a less efficient method of scattering seeds. A number of examples of the limitations of seed dispersal have been noted. In several cases where a burn had left only one or two pines upon an island the usual *Populus-Betula* association was unable to gain a foothold because of the distance from the mainland; hence these species were superseded by numerous pine seedlings. Doubtless the same principles may be applied to the relation between seed dispersal and tree migration even over greater areas. The time factor of distribution may be an expression of the rate of migration as it is determined by the method of seed dispersal.

The time factor of distribution is an expression of the rate of migration. The rate of migration is dependent upon such primary conditions as temperature, water supply, soil properties, light intensity, and methods of distribution. Time, as a condition of change in environmental factors, becomes itself of great importance in any consideration of the factors of forest distribution.

Competition factor

Competition results in the survival of the fittest. The fittest is that species or individual whose specific range of tolerance is best related to the environmental condition acting as a limiting factor toward other species; hence temperature, water supply, soil, or light may act as the basis of competition. Time may also act as a basis of competition, since it changes conditions in environmental factors. In order that competition may act as a distributional factor, conditions must be favorable for one or more species and unfavorable for others. While the time factor is an expression of the rate of change of the environmental factor acting in a limiting capacity, the competition factor is an expression of the relation between the ranges of tolerance of the forms in question toward the limiting environmental factor.

The encroachment of the deciduous hardwood forest of Ontario upon the coniferous forest is accompanied by competition. The progressive changes in such conditions as humus content of the soil and light intensity are such as to increasingly favor the former association to the detriment of the latter. *Abies*, for instance, grows readily on good soil, but it cannot tolerate the shade of an *Acer* forest. The competition becomes too great; in other words, the changes in environmental factors have been such that the mean of the range of tolerance of *Acer* more closely approximates existing conditions than that of *Abies*. The factor of competition plays its chief rôle in the so-called transition areas, where the specific ranges of tolerance of the species concerned all include existing conditions although unequally. That species dominates, other things being equal, whose mean of tolerance more nearly approximates environmental conditions.

Specific ranges of tolerance

The specific ranges of tolerance of some of the dominant forest species of Ontario, together with their relation to limiting factors, will be considered. Many of the data are represented diagrammatically in the accompanying diagrams (figs. 3–6). These diagrams summarize data collected regarding the specific ranges of tolerance of a number of forest species. In preparing the temperature diagrams (fig. 3), for example, other factors have been eliminated by selecting data respecting localities where other conditions have been favorable; in this way the maxima and minima have been determined. The diagrams are relative rather than quantitative, hence they suggest a field of research which would supply absolute numbers. When the maxima and minima have been determined, the means are represented by the mid-points of the lines joining these extremes. The radii of the circles of which the lines joining the extremes are diameters represent the magnitudes of the specific ranges of tolerance. The comparative areas of distribution as determined by the several limiting factors are represented, theoretically, by circles whose centers are the means of their ranges of tolerance and whose radii are the lines representing those ranges.

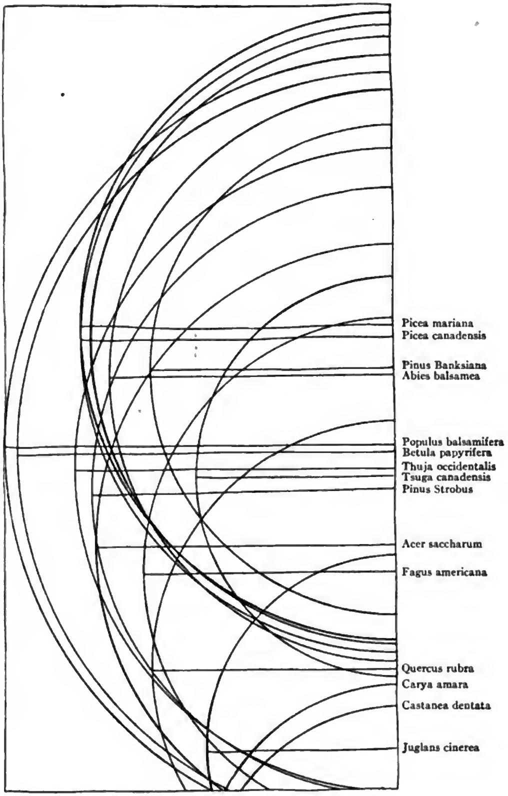

FIG. 3.—Forest trees: specific ranges of tolerance with respect to temperature

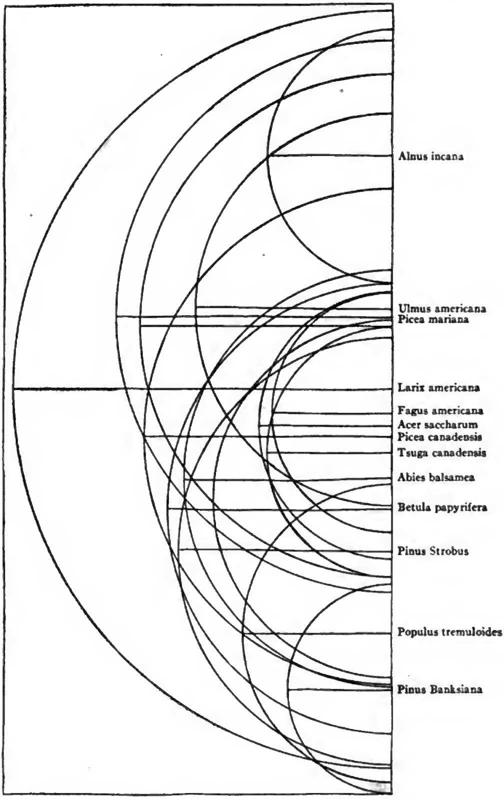

Fig. 4.—Forest trees: specific ranges of tolerance with respect to water

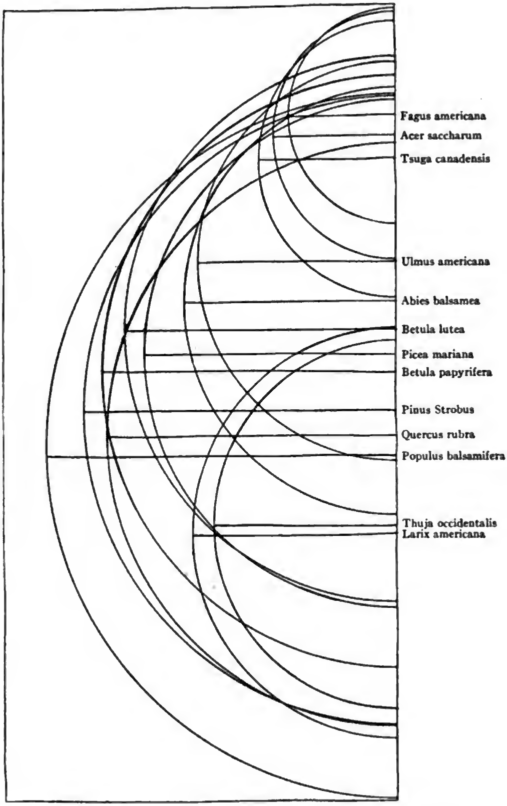

FIG. 5.—Forest trees: specific ranges of tolerance with respect to soil development

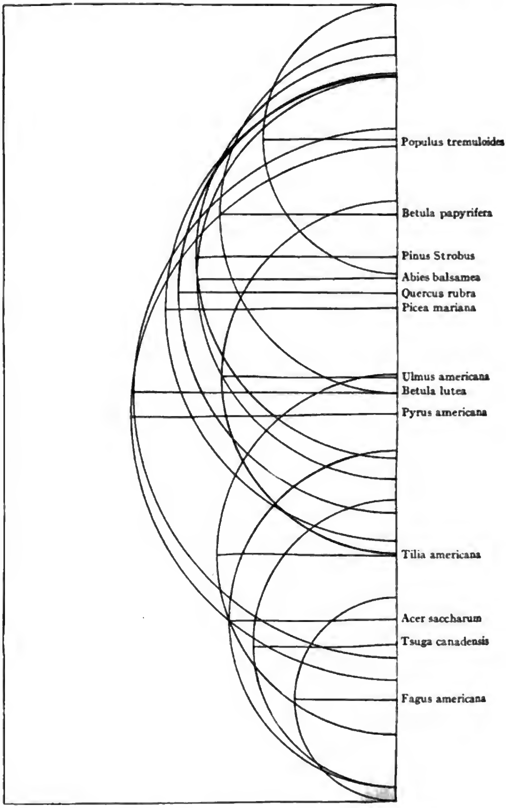

FIG. 6.—Forest trees: specific ranges of tolerance with respect to intensity of light

ABIES BALSAMEA.—*Physical factors.*—"Moisture and temperature are the main factors influencing the distribution of *Abies balsamea;* it requires a cold climate and a constant supply of moisture at its roots; a mean annual temperature not exceeding 40° F. with an average summer temperature of not more than 70° F. and a mean precipitation not less than 25 inches evenly distributed throughout the year are the necessary conditions for its growth" ZON (**27**). The maximum of its range of temperature tolerance is high, very closely approximating that of *Picea;* the minimum is lower than has generally been conceded, other factors having practically eliminated it from the warmer regions of its normal temperature range. While *Abies balsamea* normally has a wide water range, it seldom thrives except in a moist soil because this hinders the growth of a fungus which in a drier soil attacks the roots ("ground rot"). Southward *Abies balsamea* "attains its best growth and largest sizes on flats the soil of which is usually a moist deep sand loam" (ZON **27**), while "southwest of Hudson Bay it grows only in the warmest and best soils and is entirely wanting in the cold swampy tracts" (LOW **18**). *A. balsamea* demands comparatively high light intensity; seedlings are seldom found except in clearings caused by windfall, or otherwise. Generally, *Abies* has a wide range of tolerance.

Competition factor.—Northward *Picea* is the chief competitor of *Abies;* their ranges of tolerance are similar, the maxima and minima of *Picea* generally being more extreme; consequently *Abies* under most conditions would be secondary were it not for the fact that near the mean of their ranges *Abies* grows more rapidly than *Picea*. Southward the chief competitors are *Acer* and *Tsuga*. These forms have the advantage of being more shade tolerant, and hence they gradually encroach upon and finally exterminate *Abies*, which demands greater light intensity (fig. 7).

Time factor.—The northward migration of *Abies balsamea* is conditioned by temperature, and since the magnitude of temperature changes is dependent upon time, it is evident that the time factor has a bearing upon distribution. The distribution southward is affected by competition of such forms as *Acer* and *Tsuga*. Time is necessary for the environmental changes which produce

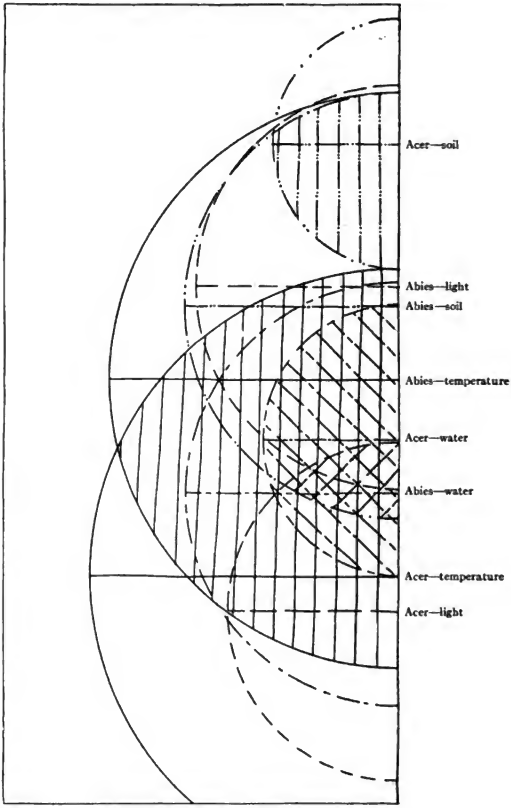

FIG. 7.—Competition areas of *Abies balsamea* and *Acer saccharum* shown by superimposing specific areas of tolerance toward factors of temperature, water, soil, and light; overlapping areas barred, the bars being similar to radii representing ranges of tolerance; barred areas represent areas of competition.

conditions more nearly approximating the mean of the range of tolerance of these competitors, thereby contributing toward the elimination of *Abies*.

The problem which arises by the appearance of *Abies* in swamps south of its "normal" range may be explained by regarding soil rather than temperature as the limiting factor. Soil changes have been slower in the undisturbed humus and rock soil layers of the swamp than on the weathered uplands. Soil conditions approximating the mean of the range for *Abies* have been maintained, hence this form has persisted; also, the presence of abundant water inhibits the attacks of parasitic fungi, thereby permitting the growth of *Abies*.

PICEA MARIANA AND P. CANADENSIS.—Although these species are closely related morphologically, they are quite different ecologically; in this respect *P. canadensis* is quite closely associated with *Abies balsamea*. *P. mariana* has a wider range of tolerance than either. Low states, "In Labrador (and northern Quebec) the white spruce grows on rich intervale grounds or near the shores of lakes and rivers. The black spruce is found on hills and in cold swamps. The two kinds have the same geographical range northward." Soil development and soil water frequently become limiting factors, separating these species. The status of temperature as a factor in distribution is demonstrated by the differences existing between *Picea mariana* and *P. canadensis*. Although they have practically the same temperature range, the latter is not found throughout a vast area of the region lying between Hudson Bay and Labrador. Available accounts and the evidence given by its habitat in other regions indicate that soil development is the limiting factor. In this respect *Abies balsamea* takes a position intermediate between these two species of *Picea*. *Picea* has previously been referred to as the chief competitor of *Abies*.

LARIX AMERICANA.—This species has a very wide range of tolerance toward temperature, water, and soil conditions. BELL (2) states "That it has an equally thrifty growth in the country to the south of James Bay and westward toward Lake Winnipeg. In this great region it attains its greatest perfection in the dry uplands and in good soil near the rivers, but smaller trees with small black spruces grow everywhere on the low swampy grounds. South of the Ottawa River it grows principally on low and level land." Low states, "*Larix* is probably the hardiest tree of the subarctic forest belt. Throughout the interior it is found in all the cold swamps and is always the largest tree in the vicinity. Along the northern margin of the forest the larch continues a tree to the very edge where the black spruce is dwarfed to a mere shrub. *Larix* demonstrates the principle that a tree which has a wide range of tolerance does not flourish in competition with species of smaller range, but is crowded into situations where conditions exclude competitors. Such a form is usually of slow growth compared with forms which are more specialized. *Larix* cannot be called a xerophyte, a hydrophyte, or a mesophyte, since it may be any of the three. Although it is usually found under extreme conditions, it grows best under mean conditions, provided competitors have been eliminated. The distribution of *Larix* is accounted for by its wide range of tolerance, together with its low status in the competition scale."

THUJA OCCIDENTALIS.—The "anomalous" distribution of *Thuja occidentalis* defies explanation by regarding temperature, water, or soil as the limiting factors (figs. 1, 2). "It is absent in Newfoundland, Cape Breton, Nova Scotia, and the east half of Prince Edward Island, but unusually large and fine in New Brunswick and the Gaspé peninsula, in which the climate, soil, etc., are the same as in the adjacent regions, where no trace of the species is to be found." BELL (2) also states that "there is a remarkable outlier of white cedar brushwood around Cedar Lake on the upper part of the Saskatchewan River at a distance of 190 miles to the northwest of the nearest point of the main area covered by this species." Moreover, it is notable that throughout great areas, for instance the Temagami region, *Thuja* is unknown, while in the surrounding country it is abundant. *T. occidentalis* has a wide range of tolerance toward environmental conditions. The presence of "outliers" where conditions are similar to those prevailing in other regions where it ordinarily occurs indicates that the general area of its distribution does not extend to its ecological limit, in many instances at least. The northern area of its distribution is roughly outlined by a semicircle, a fact which contributes evidence that *Thuja* has migrated radiately from a limited area. The method of reproduction is such that it does not migrate rapidly; that a great proportion of seeds fail to develop is of importance in this connection. It would seem that the migration of this form has lagged behind changes in ecological conditions. With respect to its range of tolerance and its position in the scale of competitors under mean conditions, *Thuja* resembles *Larix*. These characters, together with the limiting action of time, account for most of the facts of its distribution.

PINUS BANKSIANA.—The tolerance of this form toward low temperatures, dry conditions, and soil poor in humus, together with its limited range toward the other extremes, place it in a unique place among the trees of the northwestern region. It is practically eliminated from the low lying lands to the south and west of Hudson Bay and James Bay, water being the limiting factor. The inconsistencies in accounts of its northward distribution in this region are the result of its occasional presence where there are higher lands between rivers. It extends northward to 56° N. lat. on the dry uplands east of Hudson Bay. Farther south, also, it is to be found only on dry rocky or sandy soil containing little humus. It is one of the pioneer forms and survives where it can avoid competition by enduring severe conditions.

PINUS STROBUS.—This species is also a pioneer among the conifers. Seedlings are seldom found except where there is a high light intensity and well drained soil. Its ranges of tolerance with respect to temperature and water do not include the extremes which characterize *P. Banksiana*. The northern limit follows a yearly isotherm (33° F.) very closely. It would seem that in this case temperature acts as a limiting factor. Because of its longevity and its towering height individuals or groves of mature trees often persist in a region where seedlings have long been eliminated by other forms which are higher in the competition scale. The pine forest is normally succeeded by such forms as *Tsuga* or *Acer* whose seedlings tolerated shade, the time factor; hence its perpetuation depends upon the maintenance of or reversion to pioneer conditions.

TSUGA CANADENSIS.—This species is among conifers what *Acer* and *Fagus* are among deciduous trees; it is a climax form. In fact, its ranges of tolerance are almost identical with those of the deciduous forms already mentioned. *T. canadensis*, when contrasted with such species as are represented by *Pinus Banksiana*, serves to emphasize the ecological diversity of conifers. BELL (**2**) states that "this tree maintains a good size to the verge of its range and always appears to terminate abruptly." Stands of mature trees are to be found as "outliers" beyond the general area of its distribution. This evidence confirms the belief that *Tsuga* is still migrating; that in many instances it has been limited by the time factor rather than by environmental factors.

POPULUS BALSAMIFERA AND P. TREMULOIDES.—Although *P. balsamifera* generally extends farther north than *P. tremuloides*, having a greater temperature range of tolerance, its northern limit passes south of the latter at 71° W. long.; soil becomes the limiting factor in this region. *P. balsamifera* "appears to confine itself to heavy clay soil of the river valleys on the modified drift of the Cambrian areas" (Low **18**), while "*P. tremuloides* is most plentiful on the unmodified glacial till of the drift ridges." The seedlings of both require a high degree of light intensity, and as such are pioneer forms. Southward they occur only where fire and other destructive agencies have restored pioneer conditions. The abundance of these species of *Populus* northward, especially south and west from Hudson Bay, would indicate that this region is biologically young.

ACER SACCHARUM.—South of the Laurentian Plateau *A. saccharum* dominates, except in the undrained lowlands. Its range of tolerance is limited to a mature soil (that is, well drained, well aerated, and containing a relatively large amount of humus intimately mixed with the rock soil) and low light intensity. The humidity of the atmosphere in Ontario is such that it is doubtful whether it ever acts as a limiting factor, other conditions being favorable. It is evident that the distribution of *Acer* is chiefly an expression of the time factor; the time required to give rise to a deep, well drained humus soil and to shade conditions, and in addition the time which is necessary to crowd out those forms which have been instrumental in providing such conditions. As mentioned before (under time factor), the time rate of change has been less in the lowlands and upon the rock outcrops of the Laurentian Plateau than upon the highland and the weathered glacial moraine. There is abundant evidence that *Acer* is migrating northward, its progress being contingent upon the time rate of soil development.

FAGUS AMERICANA.—This species has a range of tolerance toward soil conditions which is even more limited than that of *Acer*. What has already been said for *Acer* applies equally for *Fagus*, since the latter is closely associated with the former.

ULMUS AMERICANA.—This species is another form whose distribution defies explanation by considering either temperature or rainfall as limiting factors. The limit extends well into the plains and northward beyond Lake Winnipeg; it swings southward, then northward again in the region south of James Bay; then abruptly southward and again northward with no apparent dependence upon temperature or precipitation conditions. Even within its general limits it is found only where there is a clay, imperfectly drained soil; over large areas, especially throughout the Laurentian Plateau, it has not been found. "On the Missinabi or west branch of the Moose River the white elm reappears 130 miles north of its general boundary on descending to a sufficiently low elevation above the sea" (BELL **2**). Soil conditions are the chief limiting factors; on the clay soil of the lowlands, where there is poor drainage, is its favorite habitat; for this reason it is intermittingly distributed. Its reappearance north of the height of land, its occurrence in the lowlands about Lake Winnipeg, as well as many other eccentricities of this species, may be explained upon this basis.

BETULA LUTEA.—This species may be associated with pioneer forms such as *B. papyrifera* or climax forms such as *Acer*. "Yellow birch is the most abundant hardwood in New England" (**12**), while in the lake region it is seldom seen; it becomes more abundant in the Laurentian region. "It grows in forests of widely different composition and shares to some extent the habits of paper birch, appearing on burns in small even-aged stands" (**12**). The seedlings are pioneer, yet, because of its comparative longevity, the species persists after such forms as *Picea*, *Abies*, and even *Acer* have established themselves. Among such forms only mature trees are to be found. These characters explain its distribution. In New England and the Laurentian region the time rate of change has been small. The forms which will eventually succeed this species have not had time to eliminate it. On the glacial moraine of the lake region this process of crowding out has in most places reached completion.

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NOTES ON NORTH AMERICAN TREES. III. TILIA. II

C. S. SARGENT

8. TILIA NEGLECTA Spach, Ann. Sci. Nat. II. **2**:140, *t. 15.* 1834; Hist. Vég. **4**:29. 1835.—*Tilia americana* Curtis, Rep. Geol. Surv. N. Car. **3**:79 (not Linnaeus). 1860; *Tilia pubescens* Watson and Coulter, Gray's Man. ed. 6, 71 (in so far as relates to Long Island) (not Aiton). 1889; Sargent, Silva N. Am. **1**:55 (in so far as relates to Long Island). 1891; Robinson, Gray Syn. Fl. $\mathbf{1}^1$:343 (in so far as relates to Long Island). 1897; Britton and Brown, Ill. Fl. **2**:414 (in so far as relates to Long Island). 1897; *Tilia Michauxii* Sargent, Man. 673. *fig. 549* (not Nuttall). 1903; Robinson and Fernald, Gray's Man. ed. 7. 565. 1908; Britton and Brown, Ill. Fl. ed. 2, 513 (probably in part). 1913.—Leaves thick and firm, acute or abruptly narrowed and long-pointed at apex, obliquely concave or unsymmetrically cordate at base, coarsely serrate with straight apiculate teeth pointing forward, dark green, smooth, glabrous and lustrous above, covered below except on the midribs and veins more or less thickly with short gray pubescence often slightly tinged with brown, and furnished with conspicuous tufts of axillary hairs, usually 11–14 cm. long and 6–11 cm. wide; petioles stout, glabrous, 3–6 cm. in length. Flowers about 1 cm. long, on pubescent or nearly glabrous pedicels, in long-branched, slender, glabrous, mostly 5–15-flowered corymbs; peduncles slender, glabrous, the free portion 3–4 cm. in length, the bract nearly sessile or raised on a stalk up to 1.5 cm. in length, gradually narrowed and cuneate or unsymmetrically cuneate or rounded at base, rounded at apex, glabrous, 1–2 cm. wide and 7–15 cm. long, longer than the peduncle; sepals broadly ovate, acute, ciliate on the margins, glabrous on the outer surface, covered on the inner surface with long white hairs, about half as long as the lanceolate petals, rounded and notched at apex and rather longer than the spathulate staminodia; stamens included; style villose toward the base. Fruit ellipsoidal, ovoid, obovoid, or depressed-globose, rounded or acute or rarely gradually narrowed

and acuminate at apex, rarely 5-angled, covered with rusty or pale pubescence, usually 8–10 cm. in diameter.

A tree 25–30 m. high, with a trunk sometimes 1 m. in diameter, smooth, often pendulous, branches forming a broad round head, and slender glabrous branchlets. Winter-buds ovoid, rounded at narrowed apex, about 5 mm. long, with glabrous, red-brown or light brown scales. Bark of the trunk about 2.5 cm. thick, deeply furrowed, pale reddish brown and covered with small thin scales. Flowers at the north in July and southward about a month earlier. Fruit ripens in September.

Rich moist soil, Province of Quebec, near Montreal, to the coast of Massachusetts and New York, through the middle states to the valley of the Potomac River and along the Appalachian Mountains to those of North Carolina, and to Iuka, Tishimingo County, Mississippi, and from central and western New York to northern and southwestern Missouri (*B. F. Bush*, Noel, May 27 and October 8, 1909, nos. 5765, 5983; *E. J. Palmer*, Elk Springs, McDonald County, no. 4285; limestone cliffs, Current River, Van Buren County, July 4, 1914, no. 6180).

Although I have not seen a type specimen of SPACH's *T. neglecta*, his description can only refer to this tree, which seems to have been understood only by SPACH, whose description was made from trees cultivated in France. The younger MICHAUX must have seen it in western New York, where he found what he called *T. americana* between Batavia and New Amsterdam forming two-thirds of the forest growth. In western New York, however, *T. neglecta* is a much more common tree than *T. glabra*. GRAY, too, must have been familiar with *T. neglecta*, for it is common in central New York where as a young man he did most of his field work, and in his descriptions of *T. americana* he always says "essentially glabrous," which would indicate that it might not be always glabrous. It was mistaken for *T. glabra* by CURTIS as it seems to replace that species south of Maryland. Specimens of a tree of *T. neglecta* growing near Wading River, Long Island, have been referred by many authors to *T. pubescens* Aiton, and other authors have followed me in considering the tree which I now consider *T. neglecta* to have been the *T. Michauxii* of NUTTALL, which is the *T. argentea* of MICHAUX.

In the shape and serration of the leaves and in the size and structure of the flowers and fruit there is little by which *T. neglecta* can be distinguished from *T. glabra*, but as the absence or presence of pubescence or tomentum on American species of *Tilia* is so important in distinguishing species, and as the pubescence on the lower surface of the leaves of *T. neglecta* is so constant and so persistent throughout the season, it seems best to consider it a species rather than a pubescent form of *T. glabra*. The base of the style of *T. neglecta* is furnished with long hairs and that of *T. glabra* appears to be quite glabrous. I find a slight pubescence on a branchlet from the upper part of a tree collected by CURTIS and COIT near Ithaca, New York. SPACH describes the fruit of his species as subpentagynous, and his figure represents a fruit with 5 distinct ridges. I have not seen such fruits on any specimens of wild trees, but they occur on two specimens of cultivated trees in the herbarium of the Arboretum, one from Germany and the other from Rochester, New York. On a tree cultivated in Goldsboro, North Carolina, the fruit is ellipsoidal and borne in unusually long-branched clusters.

9. TILIA CAROLINIANA Miller, Dict. ed. 8. 1758.—*Tilia pubescens* Aiton, Hort. Kew. **2**:229. 1789; Ventenat, An. Hist. Nat. **2**:68. 1800; Mém. Acad. Sci. Paris **4**:10. *t. 3.* 1802; Elliott, Sk. **2**:3. 1824; *Tilia multiflora*, Hort. ex Ventenat in An. Hist. Nat. **2**:64. 1800; *Tilia pubescens* var. *leptophylla* Ventenat, *l. c.*; *Tilia leptophylla* Small, Fl. Southern States 762 (in part?). 1911.—Leaves ovate, oblique and truncate or cordate at base, abruptly long-pointed at apex, coarsely dentate with broad apiculate glandular teeth pointing forward, and coated below with a rusty or pale easily detached pubescence of fascicled hairs; when they unfold coated with hoary tomentum, soon glabrous on the upper surface, and at maturity dark yellow-green and lustrous above, 7–15 cm. long and 6–12 cm. wide; petioles stout, glabrous, 2.5–4 cm. in length. Flowers 6–7 mm. long, on slender pubescent pedicels, in small stout-branched, pubescent, mostly 8–15-flowered corymbs; peduncle slender, pubescent, the free portion 2–3 cm. long, the bract nearly sessile, oblong-obovate, cuneate at base, rounded or acute at apex, when it first appears nearly glabrous on the upper surface, pubescent becoming glabrous or almost glabrous below, 2 cm. wide, longer or shorter than the peduncle; sepals ovate, acuminate, ciliate on the margins, brown and covered with pale pubescence on the outer surface, coated on the inner surface with long white hairs; petals lanceolate, acuminate, a third longer than the sepals; staminodia oblong-obovate, rounded at apex, rather shorter than the petals; style tomentose at base or glabrous. Fruit subglobose, ellipsoidal or obovoid, 7–9 mm. in diameter.

A large tree with slender, red-brown, glabrous or slightly pubescent branchlets. Winter-buds ovate, acute, glabrous or rarely pubescent, 5–6 mm. long.

NORTH CAROLINA.—Wrightsville Beach, New Hanover County, *W. W. Ashe* (no. 261); Wilmington, New Hanover County, *T. G. Harbison*, June 21, 1915, May 2, 1916 (nos. 6, 8, 11, 12).

South Carolina.—Near Charleston and on James Island, *T. G. Harbison*, June 17 and 18 and September 6, 1915 (nos. 1, 7, 8, 13, 14, 1*a*), September 4 and 5, 1916 (nos. 15, 17, 18), May 1, 1917, June 3, 1918 (nos. 45, 46, 47, 48); Calhoun Falls, Abbeville County, May 26, 1918 (no. 17).

Georgia.—Colonel's Island, near Dunham, Liberty County, *T. G. Harbison*, September 8 and 9, 1916 (nos. 3, 7), June 19, 1917 (no. 18), *Miss Julia King*, October 1917.

Louisiana.—Avery Island, Iberia Parish, *R. S. Cocks*, October 18, 1910 (no. 6), May 24, 1914, May 29, July 28, 1916 (nos. 4040, 4054), *Miss McIlhenny*, June 1915; Welsh, Jeff Davis Parish, *E. J. Palmer*, May 17, September 10, 1915 (nos. 7675, 8494); Opelousas, St. Landry Parish, *C. S. Sargent*, March 25, 1917; Little Bayou Têche, east of Opelousas, *R. S. Cocks*, April 3, July 24, 1916 (nos. 4012, 4016, 4018); rich woods near Winnfield, *C. S. Sargent*, April 6, 1913; Lake Charles, Calcasieu Parish, *C. S. Sargent*, April 10–13, 1915, *R. S. Cocks*, May 21, June 1, 1915 (no. 2530); Natchitoches Parish, Natchitoches, *R. S. Cocks*, April 15 and 27, 1911, *E. J. Palmer*, April 17 and 23, May 3, June 10 and 14, July 10, September 30, 1915 (nos. 7397, 7474, 7946, 7952, 8013, 8021, 8747, 9416); Creston, *E. J. Palmer*, April 28, 1915 (no. 7420); Chopin, May 6, 1915 (no. 7554).

Arkansas.—Fulton, Hempstead County, *B. F. Bush*, October 4, 1909 (no. 5926); Gum Springs, Clark County, *E. J. Palmer*, June 20, 1915 (no. 8074).

Texas.—Palestine, Anderson County, *E. J. Palmer*, September 21, 1917 (no. 12816); Marshall, Harrison County, June 8 and September 26, 1915 (nos. 7910, 8673), March 29, 1918 (no. 1320); Groesbeck, Limestone County, June 1, 1915 (no. 7934); Jacksonville, Cherokee County, June 4, 1915 (no. 7871); Larissa, Cherokee County, April 7, 1916 (nos. 9374, 9381); Houston, Harris County, September 15, 1917 (no. 12759); San Augustine, San Augustine County, April 19 and September 8, 1916 (nos. 9498, 10637); near Pledger, Matagorda County, May 8, 1916 (nos. 9698, 9704); Dayton, Liberty County, May 25, 1915 (no. 7767); Blanco, Blanco County, June 4, 1917 (no. 12165); near Boerne, Kendall County, *S. H. Hastings*, 1911, *C. A. Schattenberg*, 1915, *C. S. Sargent*, 1915, *E. J. Palmer*, September 29, 1916 (no. 10866), April 20, 1917 (no. 10866).

Mexico.—Botteri, "998 Juni 55, Orizaba" (in Herb. Kew), Orizaba, 63, 1869 (in Herb. Kew), Pr. el Chica, *C. Erenberg* (in Herb. Kew, with slightly pubescent branchlets and winter-buds).

Miller's specimen of his *T. caroliniana* from a tree cultivated in England, where it had been introduced from Carolina by Catesby, is preserved in the British Museum, the name being written on the sheet in Miller's handwriting. This specimen is also the type of Aiton's *T. pubescens*, that name also appearing on the sheet in Aiton's or Dryander's handwriting. This specimen has glabrous branchlets, coarsely serrate leaves, very oblique and truncate at base, and covered below, like the corymbs, with rusty pubescence. The leaves are rather smaller than those of the trees now growing about Charleston Harbor, as might be expected in the case of a tree from the southern states cultivated in England. There is no other linden in the South Carolina region which at all agrees with MILLER's specimen, and his name can properly be taken up for this tree. *T. caroliniana* has usually been considered a synonym of *T. americana* Linnaeus, and *T. pubescens* has been adopted for one of the southern coast species. This name, however, except as a synonym of *T. caroliniana*, must now disappear.

The leaves of the specimens collected west of the Mississippi River which are here referred to *T. caroliniana* are certainly not thinner than those from the Carolina coast region, and I can find no characters by which the eastern and western trees can be distinguished. As here understood the range of *T. caroliniana* is remarkable, as there is no evidence that it occurs between the coast of Georgia and western Louisiana.

TILIA CAROLINIANA var. **rhoophila,** n. var.—*Tilia pubescens* Torrey and Gray, Fl. N. Am. 1:240 (insomuch as relates to Texas). 1842; *Tilia pubescens* Sargent, Silva N. Am. 1:55 (insomuch as relates to Louisiana and Texas). 1891, and later authors; *Tilia pubescens* var. a *Aitonii*, V. Engler, Monog. Tilia, 128 (insomuch as relates to Texas specimens). 1909.—Differing from the type in its pubescent branchlets and winter-buds, its usually larger leaves, and in its tomentose corymbs of more numerous flowers. Leaves broadly ovate, oblique and truncate or cordate at base, abruptly short-pointed and acuminate at apex, coarsely serrate with broad apiculate teeth pointing forward, dark green and lustrous on the upper surface, pale and thickly covered on the lower surface with persistent white or brownish pubescence, 10–12 cm. long and 7–12 cm. wide, with slender midribs and primary veins pubescent on the lower side and small conspicuous axillary tufts of pale hairs; petioles stout, thickly coated with pubescence, 2.5–4 cm. in length; on vigorous shoots leaves often 16 cm. long and 14 cm. wide, and occasionally 24 cm. long and 18 cm. wide. Flowers 5–6 mm. long, on short, hoary tomentose pedicels in wide, thin-branched, pubescent, many-flowered (sometimes 50) corymbs; peduncle thickly covered with fascicled hairs, the free portion 3.5–5 cm. long, the bract oblong, unequally rounded at base, rounded at apex, glabrous on the upper, pubescent on the lower surface, 1.5–2 cm. wide, usually shorter than the peduncle; sepals acuminate, coated on the outer surface with pale or slightly rusty pubescence, villose and furnished at base on the inner surface with tufts of long hairs; petals lanceolate, acuminate and ciliate at apex, about a third longer than the sepals; staminodia spatulate, acute, about half the length of the petals; style coated at base with long white hairs. Fruit subglobose, covered with rusty tomentum, 7–8 mm. in diameter.

A tree with slender branchlets thickly coated during their first year with pale pubescence, dark red-brown or gray and puberulous during their second season. Winter-buds covered with pale pubescence.

ARKANSAS.—Fulton, Hempstead County, *E. J. Palmer*, June 17, 1915 (no. 8023); Gum Springs, Clark County, June 21, 1915 (no. 8074).

LOUISIANA.—Bank of the Calcasieu River, Lake Charles, Calcasieu Parish, *R. S. Cocks*, May 21, 1916 (no. 2532), *C. S. Sargent*, March 23, 1917; low woods, Welsh, Jeff Davis Parish, *E. J. Palmer*, May 17, June 21, and September 10, 1915 (nos. 7674, 8074, 8500).

TEXAS.—Houston, Harris County, *F. Lindheimer*, 1842 (no. 10830 in Herb. Missouri Bot. Gard.), *E. J. Palmer*, May 24 and 26 and September 17, 1915 (nos. 7758, 7776 type for flowers, 8578), April 29, 1916 (no. 9613), April 2, May 16, 17, 18 and September 15, 18, 1917 (nos. 11142, 11443, 11448, 11451, 11454, 11911, 11912, 11913, 11914, 11916, 11917, 11918, 11933, 11934, 11946, 11964, 12755, 12756, 12758, 12762, 12788), March 19, 29, 1918 (nos. 13114, 13115); Harrisburg, Harris County, *E. J. Palmer*, May 17, 1917 (no. 11933); Morgan's Point, Harris County, *E. J. Palmer*, May 20, 1917 (no. 11957); near Pledger, Matagorda County, *E. J. Palmer*, May 8, 1916 (no. 9695); Dayton, Liberty County, *E. J. Palmer*, May 25 and September 16, 1915 (nos. 7672, 7767, 7770, 8548, 8564, 8566), April 28, 1916 (nos. 9603, 9604, 9605, 9607), April 3, May 21, and September 17, 1917 (nos. 11457, 11458, 11460, 11465, 11466, 11975, 11976, 11982, 11984, 12776, 12777, 12778, 12779 with bracts of the peduncles 10–11 cm. long and 3.5 cm. wide); Palestine, Anderson County, *E. J. Palmer*, May 29, 1917 (no. 12086); Marshall, Harrison County, *B. F. Bush*, August 9, 1901 (no. 659), *E. J. Palmer*, June 8, 1915 (no. 7922); College Station, Brazos County, *E. J. Palmer*, April 28, 1917 (nos. 11720, 11721); Bryan, Brazos County, *E. J. Palmer*, April 28, 1917 (no. 11721); Liberty, Liberty County, *E. J. Palmer*, May 22, 1915 (no. 7735), April 28, 1916 (no. 9594); Livingston, Polk County, September 12, 1916 (no. 10697), September 19, 1917 (no. 12798); New Braunfels, Comal County, *F. Lindheimer*, 1842 (no. 10839 in Herb. Missouri, Bot. Gard.); rocky banks of the Guadalupe River, Kerrville, Kerr County, *E. J. Palmer*, April 29, 1916 (nos. 9931, 9934).

Growing usually on the margins of sandy bogs and on moist sandy hillsides, this tree varies, according to the moisture it obtains, in the size of the leaves and in the amount of the pubescence on the branchlets. The bark on trees growing in wet situations is smooth and pale, but on trees in dry soil or higher on the hillsides it is dark and rough; the leaves are smaller and the branchlets are less pubescent.

10. **Tilia texana**, n. sp.—*Tilia pubescens* var. β *Ventenatii* V. Engler Monog. Tilia 129 (in part). 1909.—Leaves thin, oblong-ovate, abruptly contracted into long slender acuminate points, cordate or obliquely cordate at base, finely dentate with broad apiculate teeth; early in the season pubescent above with scattered fascicled hairs and covered below with brownish, slightly attached pubescence, and in the autumn light yellow-green, lustrous and nearly glabrous on the upper surface, slightly pubescent on the lower surface, 10–14 cm. long and 8–10 cm. wide, with slender midribs and primary veins sparingly villose on the upper side and nearly glabrous on the lower side, and small axillary tufts of brownish hairs; petioles slender, pubescent with fascicled hairs, 2.5–4 cm. in length; leaves on vigorous shoots often furnished with one or two large, lateral, acuminate, serrate lobes, more coarsely dentate and more thickly covered on the lower surface with pubescence, often 13–15 cm. long and 9–15 cm. wide. Flowers 6–7 mm. long on slender tomentose pedicels in small, villose-pubescent, mostly 7–10-flowered corymbs; peduncle slender, slightly villose-pubescent, the free portion 3–3.5 cm. in length, the bract oblong-ovate to slightly obovate, unsymmetrically cuneate at base, rounded and occasionally lobed at apex, glabrous on the upper surface, densely pubescent early in the season, later becoming nearly glabrous on the lower surface, longer or shorter than the peduncle; sepals ovate, acute, pale pubescent on the outer surface, covered on the inner surface with white hairs longer and more abundant near the base; petals lanceolate, acuminate, a third longer than the sepals; staminodia linear-lanceolate, acuminate; style hoary tomentose at the base. Fruit ellipsoidal, covered with rusty brown tomentum, 8–9 mm. long and 5–6 mm. in diameter.

A small tree with slender branchlets thickly covered during their first season with close pale pubescence, and pale and puberulous or glabrous in their second year. Winter-buds ovate, obtusely pointed, thickly covered with pale pubescence, 4–5 mm. long. On vigorous terminal branchlets the pubescence is thicker and light rusty brown.

TEXAS.—Columbia, Brazos County, *B. F. Bush*, October 18, 1900 (no. 1570), September 25, 1901 (no. 914); Houston, Harris County, *E. J. Palmer*, September 17, 1915 (no. 8578), April 29, 1916 (nos. 9608, 9610); Larissa, Cherokee County, June 3 and September 22, 1915 (nos. 7845, 8620); on Spring Creek, near Boerne, Kendall County, *E. J. Palmer*, April 7 and September 29, 1917 (nos. 11485, 12899); along the southwest bank of the Guadalupe River on the rocky talus in a canyon at the foot of a limestone bluff at Kerrville, Kerr County, *E. J. Palmer*, October 2, 1916 (nos. 10887, 10888 type for fruit), April 8 and June 9, 1917 (nos. 11495, 11501, 11502, 12212, 12213 type for flowers, 12214).

I have not seen leaves and pedunculate bracts with lateral lobes on any other American linden.

TILIA TEXANA var. **grosseserrata,** n. var.—Differing from the type in the coarse serration of the leaves, in the absence of lateral lobes on the leaves and on the bracts of the peduncles, and in the constantly pale, never rusty pubescence of the branchlets and winter-buds.

A small tree with several stems 7–9 m. high, the bark dark gray and rough near the ground and smooth and pale above, in rocky soil at the foot of a limestone bluff by a small stream forming the head of the Sabinal River, near Utopia, Uvalde County, Texas, *E. J. Palmer*, June 17, 1916 (no. 10227 type), April 10 and October 6, 1917 (nos. 11522, 12937).

At the end of their first winter the branchlets of this tree are pale pubescent, puberulous or nearly glabrous, and the winter-buds are reddish or pale brown and glabrous. This linden is interesting as the most western representative of the genus in the United States.

11. **Tilia phanera,** n. sp.—Leaves semiorbicular to broadly ovate, deeply and usually symmetrically cordate at base, abruptly short-pointed at apex, finely dentate with straight or incurved apiculate teeth; when they unfold glabrous above with the exception of a few hairs on the midribs and veins, and thickly coated below with hoary tomentum, and at maturity thin, blue-green, smooth and lustrous on the upper surface, paler and often brownish and coated with a floccose easily detached pubescence of fascicled hairs on the lower surface, 5–9 cm. wide and usually rather broader than long, with slender midribs and primary veins pubescent on the lower surface, and small axillary clusters of rusty brown hairs; petioles slender, coated when they first appear with hoary tomentum, glabrous or slightly pubescent in the autumn, 2.5–4 cm. in length. Flowers 5–6 mm. long, on tomentose pedicels in compact, villose, mostly 16–20-flowered corymbs; peduncle villose, the free portion 1.2–1.5 cm. in length, the bract longer than the peduncle,

short-stalked, obovate, cuneate at base, broad and rounded at apex, floccose pubescent on the lower surface, nearly glabrous on the upper surface; sepals acuminate, pale pubescent on the outer surface, villose along the margins and furnished at the base on the inner surface with a tuft of long white hairs, broader and shorter than the lanceolate acuminate petals; staminodia oblong-obovate, rounded at apex, style glabrous except at the base. Fruit ellipsoidal, covered with rusty tomentum, 8–10 mm. long and 6–7 mm. wide, on stout, densely floccose-pubescent pedicels.

A tree with slender, light gray-brown, often zigzag branchlets covered when they first appear with fascicled hairs, deciduous during their first summer. Winter-buds ovate, obtusely pointed, terete, reddish brown, glabrous, 4–5 mm. long. Flowers the middle of June. Fruit ripens the end of September.

Banks of Spring Creek, near Boerne, Kendall County, Texas, *E. J. Palmer*, September 27, 1916 (no. 10825 type); April 7 and 11 and June 13, 1917 (nos. 11486, 11593, 12242).

TILIA PHANERA var. **scabrida,** n. var.—*Tilia pubescens* var. a *Aitonii* f. *gymnophylla* V. Engler, Monog. Tilia 130 (in part). 1909. —Differing from the type in the scabrate lower surface of the leaves. Leaves broadly ovate, cordate at base, abruptly short-pointed at apex; when they unfold pubescent above with scattered straight white hairs and hoary tomentose below, and at maturity thin, yellow-green and glabrous above and roughened below by the persistent bases of fascicled hairs, 10 cm. long and broad; petioles 2–2.5 cm. in length. Flowers not collected. Fruit on tomentose pedicels, ovoid to subglobose, covered with pale reddish tomentum.

A small tree with dark deeply ridged bark and glabrous branchlets.

On a low limestone bluff of the Blanco River, near Blanco, Blanco County, Texas, *J. Reverchon*, July 1885 (no. 1500 type), *E. J. Palmer*, April 16 and September 24, 1917 (nos. 11565, 12858); College Station, Brazos County, Texas, *B. F. Bush*, July 4, 1900 (nos. 1915, 4345); Velasco, Brazoria County, Texas, *E. J. Palmer*, March 21, 1918 (no. 13139).

12. **Tilia lasioclada,** n. sp.—Leaves ovate, abruptly contracted at apex into short acuminate points, oblique and truncate or on weak branchlets, often nearly symmetrical and deeply cordate at base, and finely serrate with straight apiculate teeth; when they unfold covered above with soft caducous hairs, pubescent below, and at

maturity thick, bright green, smooth and lustrous on the upper surface, pale and covered on the lower surface with a thick floccose, easily detached pubescence of fascicled hairs, pale on those of lower leaves and often rufous on those of upper branches, 10–15 cm. long and 8–12 cm. wide, the slender midribs and veins covered below with straight hairs mixed with fascicled hairs, and small conspicuous axillary tufts; petioles covered when they first appear with straight hairs mixed with fascicled hairs, soon glabrous, usually 3–4 cm. in length, those of the leaves of weak branchlets very slender and often 5–6 cm. long. Flowers 5–6 mm. long, on stout villose pedicels, in long-branched, mostly 10–15-flowered corymbs more or less thickly covered with straight white hairs; peduncle covered with long white hairs, the free portion 2.5–3 cm. in length, the bract nearly sessile, rounded and unsymmetrical or acute at base, rounded or acute at apex, the midrib more or less thickly covered on the lower side with straight hairs, otherwise glabrous, 2–5 cm. wide; sepals narrow, acute, pubescent on the outer surface, villose on the inner surface, about one-third as long as the lanceolate acuminate petals; staminodia spathulate, rounded and often lobed at apex, about as long as the sepals; style slightly villose at base. Fruit globose or depressed-globose, covered with rusty tomentum, about 1 cm. in diameter.

A tree sometimes 20 m. high with a trunk 30–60 cm. in diameter, stout branches forming a broad round-topped head, and stout red-brown branchlets sometimes glabrous in early summer and sometimes covered more or less thickly during their first and second seasons with long straight hairs.

South Carolina.—Calhoun Falls, Abbeville County; upland woods, Anderson County, *T. G. Harbison*, May 21, 1918; rich wooded slopes near the Savannah River, three miles below Augusta, *T. G. Harbison*, June 17 and August 23, 1916 (no. 8 type), June 17, 1917 (no. 9); Beach Island, a rich wooded slope rising from the north bank of the Savannah River a few miles below Augusta, *R. C. Berckmans*, June 12, 1914.

Georgia.—Shell Bluff on Savannah River 30 miles below Augusta, Richmond County, *C. S. Sargent*, April 6, 1914; steep rocky bluff at the Locks above Augusta, *T. G. Harbison*, May 13, 1913 (nos. 1162, 1163), May 27 and October 6, 1914 (no. 9), April 6, 1916 (no. 6), August 23, 1916 (nos. 12, 13). Brickyard near the Berckman's Nursery west of Augusta, October 5, 1914 (no. 7), August 23, 1916 (no. 16), June 29, 1917 (no. 16), May 31, 1918 (no. 31), May 30, 1918 (nos. 18, 20, 21 type).

FLORIDA.—River Junction, Gadsden County, *T. G. Harbison*, April 25 and September 21, 1914 (no. 1479), April 19 and June 25, 1917 (nos. 116, 119).

From all other American lindens this species differs in the straight hairs on the lower side of the midribs and veins of the leaves, on the peduncle and branches of the inflorescence and on the branchlets, and similar to those of the European *Tilia platyphyllos* Scopoli. The number of these hairs varies on different individuals, and on some trees the branchlets become nearly glabrous by the middle of June, while on others the hairs are present for 2 or 3 years. They are longer and more abundant on the trees growing on the Savannah River at the Locks above Augusta than on trees from other localities, and do not entirely disappear until their third season.

13. TILIA HETEROPHYLLA Ventenat.—Different plants have been referred to this species and it is still by no means clear what should be taken as the type. VENTENAT gives the locality for his tree as "la basse Caroline" where it was discovered by MICHAUX and FRASER. "Basse Caroline" may mean the coast region or the whole state east of the mountains. There is no *Tilia* in the South Carolina coast region which at all agrees with VENTENAT's description and figure, but near Augusta and in Columbia County, Georgia, and in the neighborhood of Walhalla in Oconee County, South Carolina, on the eastern foothills of the Blue Ridge, a linden is common which in the shape of the leaves agrees better with those figured by VENTENAT than any I have seen. MICHAUX in his journeys from Charleston to the high Carolina mountains went up the valley of the Savannah River and passed by Augusta and through Oconee County, South Carolina. VENTENAT describes the leaves of *T. heterophylla* as snow white on the lower surface. On the Georgia and Walhalla trees the tomentum on the lower surface of some of the leaves is white and on others, especially from upper branches, it is rusty brown, a peculiarity of this tree which is common in other parts of the country. VENTENAT describes the fruit of his tree as globose and 5-ribbed. The fruit which he figured, however, is ellipsoidal and shows no trace of ribs. If the Walhalla trees, as I believe, are to be considered typical of *T. heterophylla* Ventenat, that species may be described as follows:

TILIA HETEROPHYLLA Ventenat, An. Hist. Nat. 2:63. 1800; Mém. Inst. Paris 4:16. *t.* 5.—Leaves ovate, obliquely truncate or rarely slightly cordate at base, gradually narrowed and acuminate at apex, finely dentate with apiculate gland-tipped teeth; when they unfold pubescent on the upper surface with caducous fascicled hairs, and at maturity dark green and glabrous on the upper surface, covered below with thick, firmly attached, white or on upper branches often brownish tomentum, and usually furnished with small axillary tufts of rusty brown hairs, 8–13 cm. long and 6–10 cm. wide; petioles slender, glabrous, 3.5–4 cm. in length. Flowers 6–7 mm. long on pedicels pubescent with fascicled hairs, in wide mostly 10–20-flowered pubescent corymbs; peduncle glabrous, the free portion 2–4 cm. in length, the bract narrowed and rounded at apex, unsymmetrically cuneate at base, pubescent on the upper, tomentose on the lower surface when it first appears, becoming glabrous, nearly sessile or raised on a stalk up to 1 cm. in length; sepals acuminate, pale-pubescent on the outer surface, villose on the inner surface and furnished at base with a tuft of long white hairs; petals lanceolate, acuminate, a third longer than the sepals; staminodia oblong-ovate, acute, sometimes notched at apex; style villose at base with long white hairs. Fruit ellipsoidal, apiculate at apex, covered with rusty brown tomentum, 7–10 mm. long.

A large tree, with slender, glabrous, reddish or yellowish brown branchlets and oblong-ovate, slightly flattened, glabrous winter-buds 5–7 mm. in length, the outer scales slightly ciliate at apex.

North Carolina.—Falls of the Yadkin River, Stanley County, *J. K. Small*, August 1892; near Newbern, Craven County, *T. G. Harbison*, June 5, 1918 (nos. 42, 44 with styles villose to the middle).

South Carolina.—Walhalla, Oconee County, *T. G. Harbison*, June 4 and 22, 1915, March and October 11, 1917; Russell, Oconee County, *T. G. Harbison*, May 5 and June 29, 1917 (nos. 3, 4), July 7, 1917 (nos. 18, 20).

Georgia.—Cornelia, Habersham County, *T. G. Harbison*, July 7, 1917 (nos. 18, 20); Toccoa, Stevens County, *T. G. Harbison*, June 15, 1918 (no. 9); banks of Flint River, Albany, Dougherty County, *J. K. Small*, May 24–28, 1896, *T. G. Harbison*, June 25, 1915 (no. 3); near Zluguenin, Sumter County, *R. M. Harper*, July 11, 1901 (no. 1049); banks of Savannah River, Germain's Island, Columbia County, *R. M. Harper*, June 1, 1902 (no. 1302).

Florida.—Tallahassee, Leon County, *T. G. Harbison*, June and September 1915 (nos. 1–6); River Junction, Gadsden County, June 1915 and 1916 (nos. 1, 8, 14, 17, 18, 19, 20, 22, 23, 28, 30, 34, 36, 37, 38, 62); Rock Cave, Jackson County, *R. M. Harper*, April 28, 1910; near Marianna, Jackson County, *T. G. Harbison*, September 18, 1916 (nos. 2, 4), May 26, 1917 (no. 21).

ALABAMA.—Berlin, Dallas County, *R. S. Cocks*, June 4, 15, 1915 (nos. 780, 782), July 20, 26, 1916 (nos. 962, 970, 1012), June 18, July 25, 1918 (nos. 790, 792); near Selma, Dallas County, *T. G. Harbison*, April 20, 1915 (no. 22).

WEST VIRGINIA.—White Sulphur Springs, Greenbrier County, *Kenneth Mackensie*, no. 7532 in Herb. Mo. Bot. Gard. (*T. heterophylla* var. *microdonta* V. Engler, Monog. *Tilia*, 135).

INDIANA.—Near Vevay, Switzerland County, *C. C. Deam*, July 25, 1913, June 19 and September 8, 1915 (nos. 13808, 16159, 18806); near the Ohio River, Jefferson County, September 8, 1915 (no. 16219).

On the Florida trees the clusters of hairs at the base of the inner surface of the sepals and the hairs at the base of the style are sometimes wanting; and the fruit is subglobose, sometimes longer than broad or a little broader than long. Like the trees at Walhalla, the tomentum on the under surface of the leaves of the upper branches is usually rusty brown and silvery white on those of the lower branches.

This linden is the common species in the neighborhood of Tallahassee and River Junction, and it appears to have been usually confounded in recent years with a tree of the higher Appalachian Mountains to which I have given the name of *T. monticola*. In the size and shape of the leaves this mountain tree resembles those of *T. heterophylla*, but the tomentum on the lower surface is thicker and whiter and never brown; the petioles are longer and the flowers are nearly twice as large; the branches are red, not yellowish brown, and the winter-buds are larger, more compressed, and bright red.

TILIA HETEROPHYLLA, var. **Michauxii**, n. var.—*Tilia alba* Michaux f. Hist. Arb. Am. 3:315, *t. 2* (not Linnaeus). 1813; *Tilia heterophylla* Nuttall, Silva 1:90, *t. 23*. 1842, and of many authors insomuch as relates to the Northern States; *Tilia Michauxii* Nuttall, Silva 1:92. 1842; Britton and Shafer, North Am. Trees 688 (in part). 1908; Britton and Brown, Ill. Fl. ed. 2, 2:513 (in part), *fig. 2846*. 1913; *Tilia eburnea* Ashe, BOT. GAZ. 33:230. 1902; *Tilia apposita* Ashe, Bull. Charleston Mus. 13:27. 1917; *Tilia tenera* Ashe, *l.c.* 1917.—Differing from the type in the usually cordate, rarely obliquely truncate, more coarsely serrate leaves, broader and more abruptly acuminate at apex, and always white or grayish white, not brownish, tomentose below.

This is one of the most widely distributed of the American lindens, ranging from the valley of the Susquehanna River in Pennsylvania, where it was first noticed by the younger MICHAUX in Lancaster County, to southern and western New York, through southern Ohio and Indiana to northeastern Missouri (Ilasco, Ralls County, *John Davis*, September 30, 1914 (no. 3164), southwestern Missouri (Eagle Rock, Barry County, *E. J. Palmer*, July 16, 1914, no. 6287), and northwestern Arkansas (Eureka Springs, Carroll County, *E. J. Palmer*, September 21, 1913, no. 4412, Cotter, Marion County, September 1, 1915, no. 8405). Southward it ranges through eastern Kentucky and Tennessee to northeastern Mississippi, along the Appalachian Mountains and their foothills to northern Georgia and to southern Georgia and Dallas County, Alabama. I have not seen specimens of this linden from Illinois, although it may be expected to occur in ravines near the Ohio River in the southern part of the state.

TILIA HETEROPHYLLA var. **nivea,** n. var.—Differing from the type in the whiter tomentum on the lower surface of the leaves, the glabrous styles, in the tomentum on the lower side of the bract of the peduncle at the time the flowers open, the slightly pubescent gray or pale reddish brown branches, and in the puberulous winter-buds.

FLORIDA.—In deep woods, River Junction, Gadsden County, *T. G. Harbison*, April 19 and June 25, 1917 (no. 29 type), June 7, 1915, and June 25, 1917 (no. 27), *A. H. Curtiss*, June 4 and September 13, 1897 (no. 5875).

TILIA HETEROPHYLLA var. **amphiloba,** n. var.—Differing from the type in the fascicled hairs on the upper surface of the young leaves and in the often pubescent branchlets. Leaves broadly ovate, sometimes broader than long, abruptly short-pointed or gradually narrowed and acuminate, or occasionally rounded at apex, symmetrically or obliquely cordate or obliquely truncate at base, finely serrate with apiculate teeth; when they unfold hoary tomentose below and covered above with fascicled hairs, and at maturity thin, dark yellow-green, smooth and lustrous on the upper surface, pale green or brownish and covered below with thick, white, somewhat loose tomentum, on lateral branchlets 4–6 cm. long and 5–7 cm. wide, and on leading shoots 9–10 cm. long and 7–8 cm. wide, the midrib and primary veins covered below with fascicled hairs; axillary hairs rusty brown in small inconspicuous tufts, often wanting; petioles slender, sparingly pubescent when they first appear, becoming glabrous, 2–2.5 cm. in length. Flowers 4–5 mm. long, on stout tomentose pedicels, in broad, thin-branched, slightly pubescent, 7–25-flowered corymbs; peduncle slender, pubescent, the free portion 3–5 cm. in length, the bract oblong to oblong-obovate, cuneate at base, rounded at apex, short-stalked or nearly sessile, 7 mm.–2.5 cm. in width, thickly covered when it first appears with hoary tomentum, and at maturity tomentose on the upper and pubescent on the lower surface; sepals acuminate, densely pubescent on the outer surface, villose near the margins on the inner surface, about as long as the lanceolate acuminate petals; staminodia oblong-obovate, rounded at apex, about as long as the sepals; style slightly villose at base. Fruit ellipsoidal, covered with rusty brown tomentum, 7–8 mm. long and 5–6 mm. in diameter.

A tree 20 m. high with slender red-brown or orange-brown branchlets glabrous or sometimes covered early in their first season with fascicled hairs. Winter-buds terete, glabrous or when first formed sparingly villose, 2–3 mm. in length. Flowers at the end of June and at River Junction later than the other species with which it is associated. Fruit ripens the middle of September.

FLORIDA.—In woods in sandy soil, River Junction, Gadsden County, *T. G. Harbison*, April 26 and September 21, 1914, April 19 and June 25, 1917 (no. 1484 type), September 21, 1914 (no. 1), June 7 and 28 and September 14, 1915 (nos. 12, 13, 34, 34a, 36, 36a).

ALABAMA.—Valley Head, Dekalb County, *T. G. Harbison*, June 26, 1918 (nos. 42, 42).

I once believed that these trees could be specifically separated from *T. heterophylla*, but their close connection with that species is shown by a tree of *T. heterophylla* var. *Michauxii* which was growing near Tiptop, Tazewell County, Virginia, in May 1914 (*T. G. Harbison*, no. 1616). The upper surface of the leaves of this tree were then covered with fascicled hairs and the branchlets were glabrous. When I visited Tiptop in September of the same year this tree had been cut down, but had produced shoots from the stump which were thickly covered with fascicled hairs and bore large leaves densely pubescent on the upper surface.

14. **Tilia monticola,** n. sp.—*Tilia heterophylla*, Sargent, Silva N. Am., **1**:59 (in part, not Ventenat). *t. 27.* 1891; Man. 674 (in part). *fig. 550;* Robinson in Gray Syn. Fl. **1**^{1}:344 (in part). 1908; Small, Fl. S. States 761 (in part). 1903; Robinson and Fernald, Gray's Man. ed. 7, 566 (in part). 1908; Britton and Shafer, N. Am. Trees 686 (in part). 1908; Britton and Brown, Ill. Fl. ed. 2, **2**:512 (in part). 1913.—Leaves thin, ovate to oblong-ovate, very oblique and truncate or obliquely cordate at base, gradually narrowed and acuminate at apex, finely serrate with straight or incurved apiculate teeth, smooth, dark green and lustrous on the upper surface, thickly

coated on the lower surface with hoary tomentum, 10–17 cm. long and 8–12 cm. wide; petioles slender, glabrous, 4–7 cm. in length. Flowers 10–12 mm. long, on stout sparingly pubescent pedicels in mostly 7–10-flowered, thin-branched, glabrous corymbs; peduncle slender, glabrous, the free portion 3.5–4 cm. in length, the bract gradually narrowed and cuneate or rounded at base, narrowed and rounded at apex, glabrous, 10–14 cm. long and 2–2.5 cm. wide, its stalk varying in length from 1 to 2.5 mm.; sepals ovate, acute, ciliate on the margins, covered on the outer surface with short pale pubescence and with silky white hairs on the inner surface; petals lanceolate, acuminate, twice longer than the sepals; staminodia oblong-lanceolate, rounded at the narrowed apex, as long or nearly as long as the petals; style clothed at the base with long white hairs. Fruit ovate to ellipsoidal, covered with pale rusty tomentum, 7–8 mm. long and 6–7 mm. in diameter.

A tree rarely exceeding 20 m. in height with a trunk 1–1.10 m. in diameter, slender branches forming a narrow rather pyramidal head, and stout glabrous branchlets usually bright red during their first year, becoming brown in their second season. Winter-buds compressed, ovate, acute or rounded at apex, light red, covered with a glaucous bloom, 7–10 mm. long. Bark of the trunk 1.5 cm. in thickness, deeply furrowed, the surface broken into small, thin, light brown scales. Flowers from July 12 to July 25. Fruit ripens in September.

North Carolina.—Highlands, Macon County, at an altitude of about 600 m., *T. G. Harbison* (many specimens), June, July, and September 1915; Busbee Mountain, near Biltmore, July 5 and September 16, 1897 (ex herb. Biltmore 1030 B).

Tennessee.—Johnson City, Washington County, *Gray*, *Sargent*, *Redfield*, and *Canby*, June 21, 1877.

Virginia.—Farmer Mountain, on New River, Cornell County, *J. K. Small*. July 12, 1892, "altitude 2200 feet."

This tree has long been confounded with *T. heterophylla* and its variety *Michauxii*. From these trees it differs in its larger leaves generally more oblique at base, covered below with a denser, always silvery white, tomentum, its longer petioles, its fewer flowered corymbs and in its larger flowers which are larger than those of the other American lindens. It differs, too, in its stouter branchlets, and in the winter-buds which are red, compressed, and much larger than those of other American lindens. At Highlands, North Carolina, where this and *T. heterophylla* var. *Michauxii* are common at altitudes between 400 and 600 m., *T. monticola* flowers 10 or 12 days later than the other tree. The specimen from Johnson City, Tennessee, although it is from a much lower altitude than the others, is typical of the species, with leaves very oblique at base and up to 17 cm. long on the flowering branches; the petioles vary from 6 to 8 cm. in length. The pedunculate bract is 1.5 cm. in length. At this low altitude the trees naturally bloom earlier than at Highlands. *T. monticola*, with its large leaves snowy white on the lower surface and drooping gracefully on their long petioles, and its large flowers, is the showiest of the American lindens.

15. **Tilia georgiana,** n. sp.—*Tilia pubescens* Ventenat, Ann. Hist. Nat. **2**:62. 1800; Mém. Acad. Sci. **4**:10. *t. 3* (not Aiton). 1802.—Leaves ovate, slightly unsymmetrical at base and usually cordate on lateral branches and often oblique or truncate on leading branches, abruptly short-pointed at apex, and finely dentate, with glandular teeth pointing forward; when they unfold deeply tinged with red, covered above by fascicled hairs and tomentose below; when the flowers open dark yellow-green, dull and scabrate above and covered below with a thick coat of tomentum, pale on those of the lower branches and tinged with brown on those from the top of the tree, conspicuously reticulate-venulose, and at maturity thick, dull yellow-green, pubescent or glabrous above, rusty or pale tomentose below, sometimes becoming nearly glabrous in the autumn, 6–10 cm. long and 5–8 cm. wide; petioles slender, tomentose, 2–4 cm. in length. Flowers 6–7 mm. long, on slender pubescent pedicels in compact, slender-branched, pubescent, mostly 10–15-flowered corymbs; peduncle slender, pubescent on the lower, nearly glabrous on the upper, surface, the free portion 2.5–3 cm. in length; sepals ovate, acuminate, coated on the outer surface with pale pubescence and on the inner surface with pale hairs longest and most abundant at the base, not more than one-half the length of the lanceolate acuminate, narrow petals; staminodia oblong-obovate to spathulate, acute, about two-thirds as long as the petals; style glabrous or furnished with a few hairs at the very base. Fruit on pubescent pedicels, depressed-globose, occasionally slightly grooved and ridged, covered with thick rusty tomentum, 5–6 mm. in diameter.

A tree with slender branchlets thickly coated during their first season with pale tomentum, and dark red-brown or brown and puberulous in their second year. Winter-buds covered with rusty brown pubescence, 6–7 mm. long. Flowers the middle of June. Fruit ripens early in September.

SOUTH CAROLINA.—Near Charleston, *T. G. Harbison*, September 4, 1916 (no. 16).

GEORGIA.—Colonel's Island, near Dunham, Liberty County, *T. G. Harbison*, September 9, 1916 (nos. 4, 5, 8, 9), June 19, 1917 (no. 19); Brunswick, Glynn County, *T. G. Harbison*, May 24, June 19, September 2 and 3, 1916 (nos. 6, 7 type, 10, 11, 13, 15).

FLORIDA.—San Mateo, Putnam County, *A. H. Curtiss* (no. 401a), Gainsville, Alachua County, *T. G. Harbison*, June 10 and September 10, 1915, June 21 and September 14 and 15, 1916, April 24 and 25 and June 15, 1917; Lake City, Columbia County, *G. V. Nash*, July 11–19, 1895, *T. G. Harbison*, June 14, 1915, September 16, 1916, April 22 and June 23, 1917; Sumner, Levy County, *T. G. Harbison*, June 12, 1915, September 12, 1916, April 25, June 15 and September 25, 1917; Tallahassee, Leon County, *T. G. Harbison*, April 14, 1916; Crawfordville, Wakulla County, *R. M. Harper*, June 19, 1914 (no. 211); Marianna, Jackson County, *T. G. Harbison*, September 19, 1916 (no. 8), April 20 and May 26, 1917.

What is perhaps best considered a variety of this species may be described as—

TILIA GEORGIANA var. **crinita**, n. var.—*Tilia pubescens* Sargent, Silva N. Am. 155, *t. 26* (in so far as relates to South Carolina, not Aiton); Man. 675. *fig. 55.* 1905.—Differing from the type in the longer and more matted, usually rusty brown hairs of the pubescence, usually less closely attached to the under surface of the leaves and often very conspicuous on the young branchlets.

SOUTH CAROLINA.—Sandy woods, Bluffton, Beaufort County, *J. H. Mellichamp*, May 28, 1887; near Charleston, *T. G. Harbison*, September 6, 1915 (no. 13).

GEORGIA.—Colonel's Island, near Dunham, Liberty County, Miss *Julia King*, July 1915, *T. G. Harbison*, September 8, 1916 (nos. 1, 2).

This linden has a general resemblance to *T. Houghii* Rose, which differs in its rather looser pubescence and large and conspicuous tufts of hairs in the axils of the veins. Moreover, it hardly seems possible that a tree known only at a few stations on the coast of South Carolina and Georgia should also grow south of the City of Mexico, and so far as is now known nowhere else.

ARNOLD ARBORETUM
JAMAICA PLAIN, MASS.

THE PURPLE HYACINTH BEAN

GEORGE F. FREEMAN

(WITH SEVEN FIGURES)

Students of the genus *Dolichos* are now somewhat perplexed concerning the identity of *D. lignosus* Linn. and *D. Lablab* Linn. According to accepted usage, the former name applies to the small-leaved perennial vine sparingly grown as a greenhouse climber in northern climates and for arbors and trellises in warmer countries. CURTIS (Bot. Mag. 1797, p. 380) states that it is perennial in England. *D. Lablab* is generally understood to refer to the common hyacinth bean or Bonavist, which has large purple leaves and racemes of showy purple flowers and seeds which are mottled mahogany brown to black. There are a number of varieties of this species, some of which have white flowers, white seeds, and green leaves. The size of the seed and the length and compactness of the racemes also vary strongly in the different kinds. This plant is strictly annual in the United States. It is used as an ornamental climber for porches, summerhouses, etc.

Now PRAIN (Jour. Asiatic Soc. Bengal **66**^{2}:429–430. 1897) reverses the incidence of these names and makes *D. Lablab* refer to the perennial species and *D. lignosus* to the annual hyacinth bean.

In the 1895 edition of *Index Kewensis*, JACKSON does not recognize *Dolichos lignosus* as a valid species, but makes *D. lignosus* Jacq. Select. Am. 205 equal *D. Jacquini* DC. Prod. **2**:397, Ind. occ.; and he makes *D. lignosus* Linn. Sp. Pl. 726 equal *D. Lablab* Linn. Sp. Pl. 725, Reg. trop. Again, PIPER (U.S. Dept. Agric. Bull. 318. 1915. p. 5), evidently following PRAIN and JACKSON, accepts the validity of *D. Jacquini* DC. Prod. **2**:397 and assigns to this species the small perennial variety of *Dolichos* formerly grown in various parts of the world as *D. lignosus* Linn.

These references to LINNAEUS are to the edition of 1753, which is now the recognized beginning date of the binomial nomenclature. Evidently LINNAEUS considered these two species as distinct. If we are to follow the *Index Kewensis* in this matter we must assume that LINNAEUS was mistaken and that he had only two divergent forms out of the many varieties into which we now know *D. Lablab* to be subdivided. The evidence available, however, does not support this view, but indicates rather that the plants from which these two species were described were really specifically distinct. The original descriptions from *Species Plantarum* (pp. 725, 726) are as follows:

1. DOLICHOS leguminibus ovato-acinaciformibus, seminibus ovatis. hilo arcuato versus alteram extremitatem. *Roy. lugdb.* 368. *Hort. ups.* 214. ***Lablab***
Phaseolus aegyptius, nigro semine, *Bauh. pin.* 341.
Phaseolus niger Lablab. *Alp. aegypt.* 74. t. 75. *Vest. aegypt.* 27.
Habitat in Aegypto.
Legumina *dorso scabra.* Caules ramique *teretes, retrorsum scabri.* Pedunculi *semiverticillati.*

9. DOLICHOS caule perenni, pedunculis capitatis, leguminibus strictis linearibus. ***lignosus***
Dolichos caule perenni lignoso. *Hort. cliff.* 360. t. 20.
Phaseolus indicus perennis, floribus purpurascentibus. *Eichr. carol.* 36.
Habitat . . . .

Of the identity of *D. Lablab* L. we have no doubt. The original description corresponds exactly with the plant grown today under the name hyacinth bean. This is further confirmed by the presence in the herbarium of the Linnean Society of London of a specimen of this plant identified and written up by LINNAEUS himself. In fig. 1 is given a tracing of this specimen which was very kindly furnished by the general secretary of the Linnean Society.[1] The identity of this plant with the common hyacinth bean is evident. Compare fig. 2, which is a photograph of a specimen grown by the writer. The references given by LINNAEUS to "Bauh. pin. 341" and "Alp. Aegypt. 74 t. 75" have been examined and leave no doubt but that they refer to the common hyacinth bean. The reference to "Roy lugdb. 368, Hort. ups. 214" has not been available.

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[1] This tracing was kindly obtained for the writer by Dr. OAKES AMES of Harvard University.

The confusion has evidently arisen on account of the uncertainty as to the identity of the plant described by LINNAEUS as *D. lignosus*. There is no cut accompanying this description, but LINNAEUS refers to an earlier publication by himself (Hort. Cliff. 360. t. 20) and to "Eichr. Carol. 36." This latter publication has not been available, but the former has been examined carefully. Fig. 3 is a reproduction of a photostat copy of LINNAEUS' figure in Hort. Cliff. 360 t. 20. The description accompanying this plate was much more full and complete than that in the *Species Plantarum* of 1753, and moreover was evidently made from a

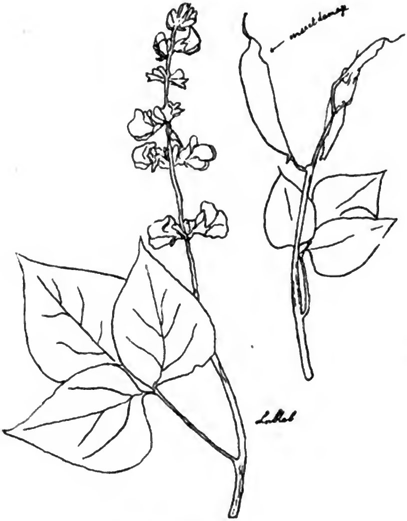

FIG. 1.—Tracing of specimen of *Dolichos Lablab* identified and described by LINNAEUS; from specimen in herb. Linnean Society.

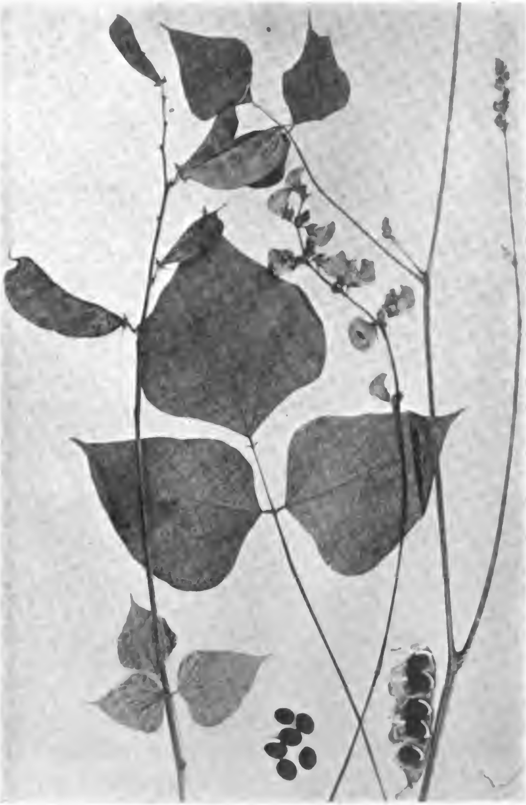

FIG. 2.—Purple hyacinth bean (*Dolichos Lablab*): photograph of specimen grown at University of Arizona, 1914.

fresh specimen before him. This description may be quoted as follows:

> 2. Dolichos caule perenni lignoso. Vide Tab.
> Phaseolus indicus perennis, floribus purpurascentibus. Hort. Carolsrb. 36.
> Crescit in America.
>
> Ante accessum nostrum enata fuit planta frutescens arcte scandens, plus quam homanae altitudinis; caule tereti, contorto, vix striato, ramis plurimis tenuibus. Folia ad ramorum exortum ternata, petiolo communi insidentia, quorum quod intermedium ovato-cordatum, acuminatum, latitudine pollicis, glabrum, petiolo proprio quaduplo reliquorum productiori insidens; lateralia latere exteriori magis dilatata, interiori vero dimidio angustiora. Flores in pedunculo pauci, corolla rubra seu purpurea. Absoluta florescentia absque fructu periit.

It should be noted in this description that although the plant was 6 ft. or more, the leaves were but 1 inch wide and are recorded as being smooth. This plant, which was probably the only specimen of *D. liguosus* actually seen by LINNAEUS, bloomed freely but did not set seed. LINNAEUS therefore probably never saw the seeds or pods of this species, but quoted the descriptions of these organs in his later publications from descriptions by other authors of plants which he assumed to be of the same species. Here in all probability lies the source of confusion. LINNAEUS had observed that his *D. Lablab* was an annual in Europe and did not know that in warmer countries this same species may persist as an herbaceous perennial. When therefore he met with a *Dolichos* which was described as perennial, he would naturally be inclined to associate it with a species of *Dolichos* which he knew to be perennial, that is, his own *D. lignosus*. Thus he made the error in the 1763 edition of *Species Plantarum* (p. 1022) of citing *Phaseolus perennis* of Rümph. Amb. 5, pp. 378 t. 136, as a synonym of his *D. lignosus*, although this species (which is clearly *D. Lablab*) is described by RÜMPHIUS, in the publication named, as having leaves 3-4 inches long and nearly as broad, with racemes 1 ft. long and bearing many flowers. RÜMPHIUS' plate, a reproduction of which is given in fig. 4, could scarcely be assumed to represent the same plant as that of *D. lignosus* in Hort. Cliff. 360. The only point of similarity is in

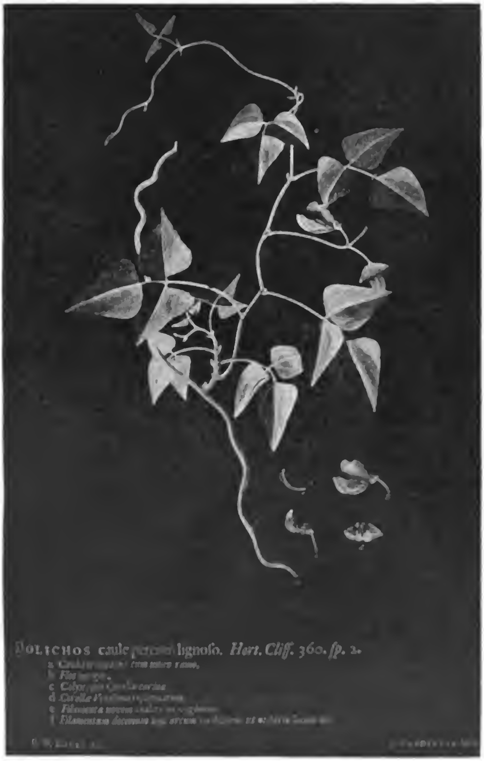
DOLICHOS caule perenni lignoſo. Hort. Cliff. 360. ſp. 2.

FIG. 3.—*Dolichos lignosus* Linn.: from photostat copy of LINNAEUS' figure in *Hortus Cliffortianus*.

the flower clusters, and here the descriptions show these to be entirely distinct (see legend to fig. 4).

Turning to the descriptions and plates left by other botanists of the immediately succeeding decades we find in JACQUIN *Selectarum stirpium Americanarum historia* (1763) a plant described as *D. lignosus.* Citations to the *D. lignosus* of Linn. Sp. Pl. 726 and Linn. Hort. Cliff. 360. t. 20 are given with question marks, indicating that the author doubted that the plant he described was the same as that described by LINNAEUS. An examination of his description makes it clear that the two plants were entirely different, for the plant of JACQUIN had pilose stems and pods, peduncles shorter than the scabrous leaves, white flowers, and pods 3–4 inches long, containing about 18 seeds, whereas, as we shall see, the plant described by LINNAEUS had nearly smooth stems, pods, and leaves, peduncles longer than the leaves, purple flowers, pods 1–2 inches long with 7 or 8 seeds at the most.

AITON (Hort. Kew. **3**:31, 33. 1789) recognizes both *D. Lablab* L. and *D. lignosus* L. and gives practically the same descriptions as are given by LINNAEUS. He states that *D. lignosus* was introduced into England in 1776 by MONF. THOUIN.

In 1792 SMITH (Spicilegium Bot. no. 2, Gleanings of Botany, pp. 19 and pl. 21) describes and pictures a plant which he calls *D. lignosus.* SMITH's plate is here reproduced in fig. 5 and his description is so clear and concise that it is quoted in full as follows:

TABLE XXI

Dolichos lignosus. Purple woody Dolichos. Diadelphia Decandria. Stigma downy.

GEN. CHAR. Standard marked at its base with two parallel oblong tubercles, compressing the under side of the wings.

Section 1. Climbers

SPEC. CHAR. Stem climbing, perennial. Flowers in little heads. Pods straight, linear.

Syn. *Dolichos lignosus* Linn. Sp. Pl. 1022. Hort. Cliff. t. 20. Ait. Hort. Kew. V. 3.33.

A native of the East Indies.

Root woody, perennial. Stem woody, supple, climbing, much branched, roundish, striated, smooth; branches alternate, very long and slender, but

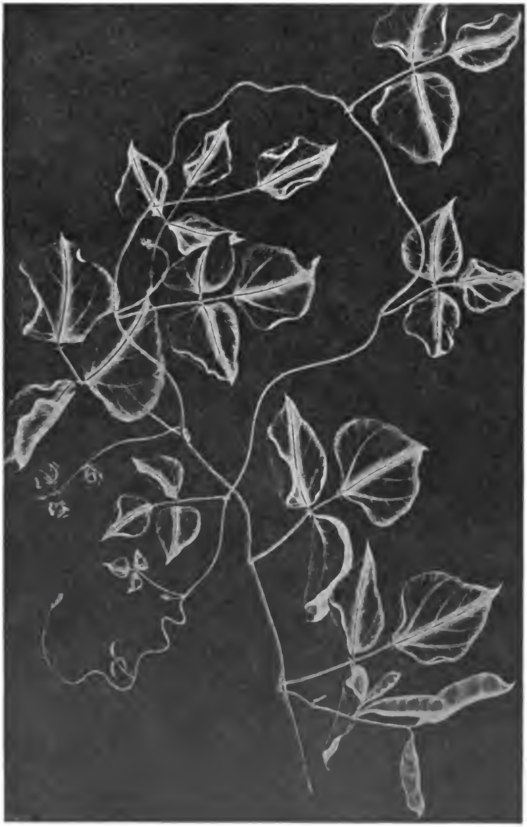

FIG. 4.—*Phaseolus perennis* Rümph. Amb. 5. 378. t. 136: the description accompanying this plate states that the racemes are 1 ft. long and many-flowered; plant here represented is undoubtedly *D. Lablab* Linn.

little subdivided, round, striated, somewhat downy, leafy, many-flowered. Leaves alternate, on long footstalks, ternate, or rather binate with an odd one.

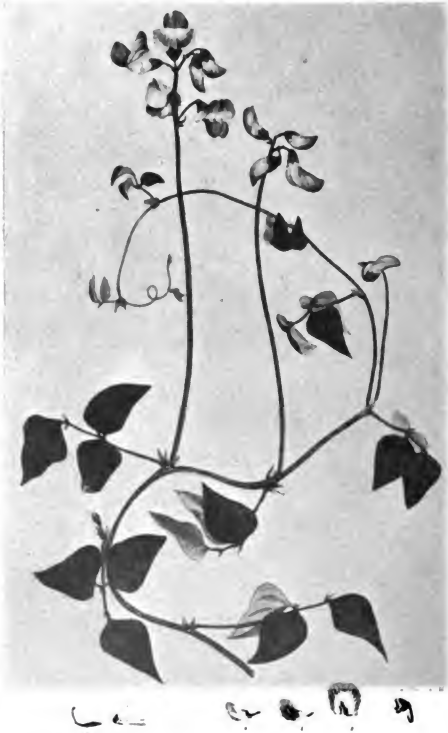

FIG. 5.—*Dolichos lignosus:* reproduction of pl. 21, J. E. SMITH, Spicilegium Bot. no. 2. Gleanings of Botany. 1792.

Common footstalk roundish, channeled above, swelling and purplish at the base; partial ones very short, swelled, incurved. Leaflets rhomboid, elongated, acute, entire, obsoletely 3-nerved; bright green and shining above; glaucous beneath. Stipulae entire, sharp, somewhat triangular, downy on the margin, dark purple at the base; of which 2 larger ones are placed at the bottom of the common footstalks, and 2 smaller, lanceolate, at the insertion of the partial footstalks. Clusters axillary, solitary, erect, each having from 3 to 6 flowers in a little head. Common flowerstalk simple, very long, striated, angular in the upper part; partial ones generally 2 together, short, downy, single-flowered.

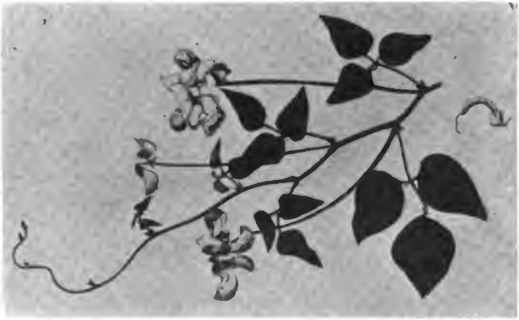

FIG. 6.—*Dolichos lignosus:* from photograph of colored plate in Curtis' Bot. Mag. 2:380. 1797.

Bracteae lanceolate, acute, hairy. Flowers somewhat drooping, rose coloured with a purplish keel. Calyx smooth, thickly ciliated in the margin. Pod an inch long, a little recurved, brownish, smooth. Seeds black.

According to Aiton, this beautiful plant was introduced from the French gardens to our own in 1776. It is easily propagated by seed, and in a stove produces abundance of flowers during the summer.

A little study of Smith's plate and descriptions shows that it agrees very closely with the plate and description of *D. lignosus* of Linnaeus and that it cannot possibly be the *D. lignosus* of Jacquin.

Five years later, in Curtis' Bot. Mag. 11:380. 1797, is found a description and plate of *D. lignosus*, which is reproduced in fig. 6.

Comparing the plate and description with those of SMITH and LINNAEUS, there is no doubt that they all had the same plant. Finally, fig. 7 is made from a fresh specimen of plants grown at the University of California. This plant agrees perfectly with SMITH's description and with every essential part of the description and plate by LINNAEUS except that in which he states that the pods are straight. When we remember that LINNAEUS probably never saw the pods of this species, such a discrepancy is not surprising.

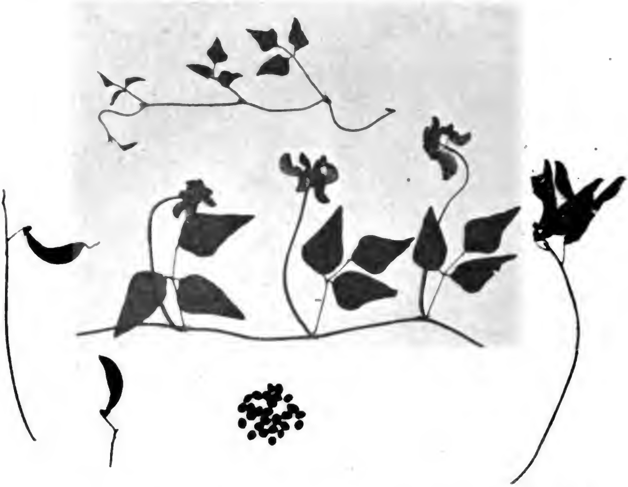

FIG. 7.—*Dolichos lignosus:* from photograph of fresh specimen furnished by Professor GREGG, University of California, January 1914.

Misled by the error of LINNAEUS in ascribing straight pods to his *D. lignosus*, DECANDOLLE (Prod. **2**:397. 1825) makes the *D. lignosus* of CURTIS (Bot. Mag. t. 382[2]) a variety of *D. lignosus* Linn. He moreover corrects the error made by JACQUIN in assigning his plant (described in Select. Stirp. Amer. Hist. 1763, p. 205) to *D. lignosus* L. by calling this plant *D. Jacquini*. To emphasize the justice of this disposition of the 2 species by DeCandolle, the original description furnished by Jacquin may be quoted as follows:

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[2] This is an error by DECANDOLLE, and should read 380.

> Planta perennis, volubilis, tota pilosa; praecipue vero rami inferiores lignosi, and legumina, pilis hispida sunt. Foliola sunt ovata, acuta, scabriuscula, duos pollices longa, lateralibus interne obliteratis. Stipulae ex lanceolato ovatae, acuminatae, basi emarginatae. Pedunculi umbellati, foliis breviores, pauciflori. Flores albidi. Legumina tres quatuorve pollices longa, acuminata, stricta, ad apicem leviter incurva, teretia, nec torosa, pilossissima fusca, interne nivea. Semina circiter octodecem, nitida, atra cum hilo albido, parva, compressiuscula, ex oblongo reniformia.
>
> Habitat in Caribaearum sylvaticis.

It would be difficult to harmonize this description with that of either Smith (Spic. Bot. no. 2, p. 19) or Linnaeus (Hort. Cliff. 360. t. 20). We must conclude, therefore, with DeCandolle, that it is a distinct species and follow him in calling it *D. Jacquini* DC. Prod. **2**:397.

In the opinion of the writer, the evidence presented herewith is sufficient to show that the plants described as *D. lignosus* by Linnaeus (Sp. Plant. ed. 1, 1753, p. 726), and more fully in his earlier work (Hort. Cliff. 360. t. 20. 1737), by J. E. Smith (Spic. Bot. no. 2, p. 19, pl. 21. 1792), by Curtis (Bot. Mag. **11**:380. 1797), and the plant now grown in various parts of the world as *D. lignosus* and shown in fig. 7 are all one and the same species, which is distinct from *D. Lablab* L. We are therefore unable to follow either Jackson (Index Kewensis 1895) in making *D. lignosus* L. a synonym of *D. Lablab* L; Prain (Jour. Asiatic Soc. Bengal **66**^{2}:429–430. 1897) in reversing the incidence of the original Linnaean names by making *D. Lablab* L. refer to the perennial species and *D. lignosus* L. to the annual hyacinth bean; or Piper (U.S. Dept. Bull. Agr. 318. 1915, p. 5), in assigning the plant commonly grown as *D. lignosus* L. to *D. Jacquini* DC. On the other hand, we must hold to the original Linnaean designation of the common annual (frequently perennial in tropical countries) hyacinth bean (and its many varieties, fig. 2) as *D. Lablab* L., and the more slender perennial greenhouse (in northern climates) climber shown in fig. 7 as *D. lignosus* L.

Agricultural Experiment Station
University of Arizona

A MORPHOLOGICAL STUDY OF PALLAVICINIA LYELLII

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 245

ARTHUR W. HAUPT

(WITH PLATES XX–XXIV)

Pallavicinia, according to SCHIFFNER's (12) census, is represented by 21 species, most of which are tropical. Later, SCHIFFNER (13) added 2 European species to his former list, thus making 5 species indigenous to the Old World. *Pallavicinia Lyellii* is found in the more humid parts of both the Northern and Southern Hemispheres; it grows near Chicago in a peat bog at Mineral Springs, Indiana. *Pallavicinia*, *Symphyogyna*, and *Monoclea* are included in the family Leptotheceae. The affinities of the Japanese genus *Makinoa*, described by MIYAKE (9), seem to place it in this family, as is done by CAVERS. The disposition of *Monoclea* is a matter of great difference of opinion, some, as JOHNSON (6), placing it with the Marchantiales. There can be no doubt, however, as to the closeness of relationship between *Pallavicinia* and *Symphyogyna*, regardless of the classification of the other genera of the family.

CAVERS (2) divides *Pallavicinia* into the two genera of GOTTSCHE: *Blyttia* and *Mörckia*. According to the Vienna code, the older name *Pallavicinia* must be retained; if SCHIFFNER's subgenus *Mörckia* (Gott.) is to be elevated to generic rank, it must not be done at the expense of the name *Pallavicinia*. STEPHANI (14) separates the genus into the 2 sections PROCUMBENTES and DENDROIDEAE; SCHIMPER, into the subgenera *Eupallavicinia*, *Mörckia*, and *Millenia*. *Pallavicinia Lyellii* belongs to the PROCUMBENTES or *Eupallavicinia* division.

Material

Most of the material studied was collected by Mr. R. P. MASON, at Columbiana, Alabama, to whom the writer is greatly indebted. Additional material was obtained by Dr. W. J. G. LAND, at Mineral Springs, Indiana. Most of the slides illustrating the antheridial series were made by Dr. LAND and Mr. MASON, while those showing the development of the archegonium and the sporophyte were prepared by the writer.

Thallus

The vegetative body of *Pallavicinia Lyellii* consists of a creeping, prostrate thallus 4–5 mm. wide, composed of a midrib with thin, one-layered, lateral wings, and bearing rhizoids. The margin is somewhat undulate, with no indications of hooked appendages as in *P. longispina*, *P. xiphioides*, or *P. Zollengeri*. The midrib consists of pitted conducting cells with thickened walls, which become differentiated directly behind the apical cell (fig. 45); about 70 to 80 may be seen in cross-section (fig. 44). TANSLEY and CHICK (15) made a careful study of these cells and showed by eosin solutions that they conduct water. Miss MCCORMICK (8) demonstrated that in *Symphyogyna aspera* they are composed of pectose. These conducting cells are also found in *Hymenophyton*.

Growth of the thallus is by means of a dolabrate (zweischneidig) apical cell (fig. 43). This feature seems to have first been observed by LEITGEB (7), who discusses at considerable length apical growth and the development of the thallus body. Two-celled mucilage hairs arise both dorsally and ventrally in connection with the apical cell, strongly resembling sex organ initials.

Branching is of two kinds: apical, from the apical cell; and endogenous, from ventral adventitious shoots. Material showing the origin of the latter was lacking and hence LEITGEB's statement, that the conducting tissue of the ventral branch is not continuous in origin with the central cells of the main thallus, could not be verified.

Sex organs

The gametophytes of *Pallavicinia Lyellii* are strictly dioecious, the male plants being slightly more slender than the female. Both antheridia and archegonia are dorsal, the former lying in 2 parallel rows on each side of the midrib, and the latter remaining directly above the midrib, slightly raised on a pad. Two involucres are present, the outer one corresponding to that of *Symphyogyna* and *Monoclea;* the inner one, or perianth, is characteristic of *Pallavicinia*, *Podomitrium*, and *Calycularia*.

ANTHERIDIA

The antheridia originate in close proximity to the apical cell, arising in acropetal succession on the dorsal side of the thallus, usually singly, but occasionally two or three together. With further apical divisions they come to lie in 2 parallel rows on each side of the midrib, slightly sunken in the thallus by the development, from behind, of an involucral upgrowth. The mature antheridia are spherical and short-stalked and point diagonally outward and upward, each one being separated from the one preceding it by sterile tissue (fig. 1).

An antheridium initial appears as a papillate projection above the surface of the thallus, resembling closely one of the mucilage hairs with which it is associated. A transverse wall appears, dividing the initial into 2 nearly equal segments, the basal one remaining in the thallus and the outer one projecting above the surface of the thallus (fig. 2). The outer cell divides transversely into equal segments, forming a primary stalk cell and a primary antheridial cell (fig. 3). With further increase in size, the latter divides by a median vertical wall, followed rapidly by a similar division in the stalk cell (fig. 4). One or two further transverse divisions complete the stalk, while a periclinal wall cuts off a peripheral cell on one side of the antheridium, intersecting the first vertical wall near the top (fig. 5). A corresponding periclinal wall appears on the other side, followed by 2 more walls at right angles to the first two, intersecting both these and the first median division. As a result, 4 primary wall cells inclose 2 central cells, the entire structure being bisected by the original vertical wall. At this stage the involucre appears as an upgrowth of the thallus behind the young antheridium (fig. 9). It is built up by basal growth, and by the time the antheridium is mature, it consists of a scalelike sheath, 6–10 cells in length. Whether these coverings are to be regarded as the beginnings of true foliar structures or merely as dorsal upgrowths of the thallus seems to be entirely a matter of opinion. If the complete involucre of *Pellia* be taken as representing the initial stage, a failure of the forward portion to develop would result in the precise condition found in *Pallavicinia*. *Sphaerocarpus*, perhaps, represents an intermediate stage, as here the development of the forward portion is slightly arrested, resulting in greater protection from behind. It seems a perfectly logical step from the antheridial condition in *Pallavicinia* to that of one of the simpler acrogynous Jungermanniales, such as *Porella*, in which case the coverings are longer and more leaflike in appearance.

Further growth of the antheridium corresponds to that of the other anacrogynous Jungermanniales. During the 2 or 3 mitoses preceding the formation of the sperm mother cells, the cell walls of the spermatogenous mass gradually disappear and abundant mucilage surrounds the dividing protoplasts. Walls around the sperm mother cells were evident, but it could not be determined whether they had been laid down by the mother cell protoplasts, or represented the remaining cellulose which had not become mucilage. The sperm mother cells produce two sperms, each with little cytoplasm, and separated by a very thin wall. The nuclei were so small that it was not possible to study the details of spermatogenesis. The development is probably the same as that of *Pallavicinia Zollengeri*, described by CAMPBELL and WILLIAMS (1).

ARCHEGONIA

The earliest stages in the development of the archegonial group were not present in the material studied. A group of initials seems to arise a short distance back of the apical cell, directly above the midrib on the dorsal side of the thallus. This group presently becomes surrounded by an annular upgrowth of the thallus, which becomes the involucre. The apical cell is not checked by the development of the archegonia, but continues the growth of the thallus, so that often 2 or 3 groups may be produced along the midrib, separated by sterile areas. The archegonial group continues to produce archegonia up to the time of fertilization, many young sex organs frequently being found with mature ones. Two-celled mucilage hairs are abundantly produced. Twenty to 30 archegonia usually occur in a group.

The archegonium, like the antheridium, arises as a papillate projection from one of the cells inclosed by the involucre. A transverse wall cuts off a basal cell, which remains within the thallus, and an outer cell, which is freely exposed (fig. 10). The latter undergoes 2 transverse divisions, the sequence of which could not be determined; the lower 2 cells form the stalk and the upper one the archegonium proper, agreeing in this repsect with *Pallavicinia radiculosa*, described by CAMPBELL and WILLIAMS (figs. 11, 12). Three vertical divisions occur in the archegonium proper, according to the manner of all anacrogynous Jungermanniales, resulting in the formation of an inner cell surrounded by 3 primary wall cells, 2 of which can be seen in a longitudinal section (fig. 12). A transverse division in the upper part of the inner cell results in the formation of a central cell and a cap cell (fig. 13), which later undergoes further division, contributing to the development of the neck.

Following the formation of the cap cell, the central cell divides into two nearly equal cells (fig. 14), the upper being the primary neck canal cell, and the lower the primary ventral cell. The development of the axial row usually precedes the division of the primary ventral cell, although frequently mitoses can be seen in the neck cells after the formation of the ventral canal cell and egg (fig. 22). In most cases about 10 neck canal cells were seen; sometimes, however, as many as 18 are formed (fig. 25). The primary ventral cell, by a transverse division, produces a ventral canal cell and egg which are almost equal in size (fig. 18). The neck canal cells are surrounded by a jacket of 5 cells, although frequently one or more of these may divide (fig. 24).

Very soon after the division of the ventral cell the ventral canal cell becomes mucilaginous and finally the entire axial row is broken down (figs. 19, 20). The egg nucleus at this stage is very prominent, the dense nucleolus being surrounded by extremely light nucleoplasm. With the preparation of the egg for fertilization, the wall of the venter becomes 2-layered, the first divisions occurring as the ventral canal cell begins to disorganize. The mature archegonium is characterized by a rather long slender stalk, a narrow venter, and a long twisted neck; it closely resembles an archegonium of *Symphyogyna*.

Just before the older archegonia in a group mature the characteristic perianth appears immediately within the involucre. It attains a height of several cells (fig. 21), but as soon as fertilization is effected, it is greatly stimulated, and develops, by basal intercalary divisions, much in excess of the young sporophyte. The perianth keeps pace with the elongation of the embryo, reaching a maximum height of about 5 mm. At the time immediately preceding spore disperal, the seta shows remarkable growth, becoming 25–27 mm. long. The perianth attains a thickness of 3 or 4 cells, as seen in cross-section, and becomes fringed around the top. The involucre, on the other hand, does not at any time exceed the height of the archegonia and it is related to their protection in the same way that the perianth is associated with the protection of the sporophyte. With the development of the perianth, following fertilization, the involucre becomes flaring and denticulate around the top.

After fertilization the egg cytoplasm becomes denser and a heavy wall is laid down around the protoplast, thus making it independent of the tissue of the archegonium.

Sporophyte

The youngest sporophyte which was observed consisted of a tier of 4 cells (fig. 26). The first division is followed by a transverse wall in the lower segment and then by a similar wall in the upper segment. A vertical division then occurs in the upper half of the embryo (figs. 27, 28), followed by vertical and transverse walls. The lower half of the embryo usually undergoes one vertical division, but contributes nothing to the development of the foot, seta, or capsule (fig. 29). Half of the potentially sporogenous tissue derived from the fertilized egg thus is diverted for haustorial purposes. A similar situation has been observed by Miss Clapp (3) in *Aneura pinguis*, and by Campbell and Williams in *Pallavicinia Zollengeri*. The relation between the early divisions in the embryo and the development of the 3 regions of the sporophyte could not be ascertained, material being wanting. The differentiation of the sporogenous tissue, however, occurs relatively late. According to Farmer (4), the young embryo of *Pallavicinia decipiens* consists of a tier of 3 cells, the upper segment forming the capsule, the middle segment the seta and part of the foot, and the lower segment the rest of the foot.

With the growth of the embryo, the venter of the archegonium becomes a calyptra 4 or 5 cells in thickness, which grows in length with the sporophyte. The calyptra is notably smaller than in *Symphyogyna* and *Monoclea*, presumably because its protective function is performed by the perianth. The non-functioning archegonia are carried up with the tissue of the calyptra but do not persist long. Only one embryo was seen developing in an archegonial group, although it is possible that more than one may be formed, as in *Symphyogyna aspera*.

The differentiation of the spores and elaters occurs late in the development of the sporophyte, and follows precisely the method of *Symphyogyna aspera*, as described by Miss McCormick (figs. 33–38). Material showing the reduction division in the formation of spores was entirely absent in the material studied. Farmer (**5**), in his study of this process in *Pellia epiphylla* and *Pallavicinia decipiens*, noted the presence of a quadripolar spindle in the spore mother cell. Moore (**10, 11**), however, working with *Pallavicinia Lyellii*, failed to find such a condition, but observed that the two divisions take place in very rapid sequence, giving the appearance of such a spindle as Farmer describes.

The mature capsule is cylindrical, is inclosed by a sterile wall one cell thick, and bears spiral thickenings (figs. 32, 39). The sterile cap at the apex of the mature capsule is not so prominent as in *Symphyogyna*, being only 5 or 6 cells thick, and bears no relation to the elaters. The mature sporophyte reaches a length of 40 mm., the capsule being about 3.5 mm. long. Dehiscence is by means of 4 longitudinal slits which remain attached at the top. The foot is wedge-shaped as in *Symphyogyna*, but it occasionally shows a resemblance to the anchor-like foot of *Marchantia* (figs. 41, 42). The mature elaters reach a length of nearly 0.3 mm., and are furnished with a double spiral band. The spores are about 0.015 mm. in diameter, the wall being conspicuously reticulate (fig. 38).

Summary

1. *Pallavicinia Lyellii* belongs to the subgenus *Eupallavicinia*, the vegetative body consisting of a single prostrate portion.

2. The apical cell is of the dolabrate type. Branching is both apical and adventitious.

3. *Pallavicinia Lyellii*, like the other species of the genus, is strictly dioecious.

4. The antheridia occur in 2 parallel rows on each side of the midrib, and are protected from behind by an involucral upgrowth. Their development, with minor variations, follows the type for the anacrogynous Jungermanniales.

5. The archegonia are in dorsal groups and are surrounded by an involucre and a perianth, the latter remaining inconspicuous until after fertilization.

6. The young archegonial stalk consists of 2 cells. The egg is small and the neck long and twisted.

7. The lower half of the fertilized egg becomes a haustorial organ and contributes nothing to the development of the foot, seta, or capsule.

8. The calyptra is 4 or 5 cells in thickness, in this respect differing from that of *Symphyogyna*.

9. The differentiation of the spores and elaters occurs relatively late in the development of the sporophyte, and follows the method of *Symphyogyna*.

10. A sterile cap is present at the apex of the capsule and remains intact in dehiscence, which is accomplished by means of 4 longitudinal slits.

To Dr. W. J. G. LAND, under whose direction the study was undertaken, the writer is indebted for many helpful suggestions and criticisms.

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EXPLANATION OF PLATES XX–XXIV

Pallavicinia Lyellii

Fig. 1.—Thallus with antheridia; ×10.

Figs. 2–7.—Stages in development of antheridium; ×630.

Fig. 8.—Older antheridium; ×62.

Fig. 9.—Young antheridium with involucre; ×46.

Figs. 10–20.—Stages in development of archegonium; ×520.

Fig. 21.—Perianth before fertilization; ×50.

Fig. 22.—Archegonium showing elongation of neck; ×50.

Fig. 23.—Median longitudinal section of archegonial group; ×25.

Fig. 24.—Cross-section of neck of archegonium; ×520.

Fig. 25.—Mature archegonium showing 18 neck canal cells; ×260.

Figs. 26–28.—Stages in development of embryo; ×520.

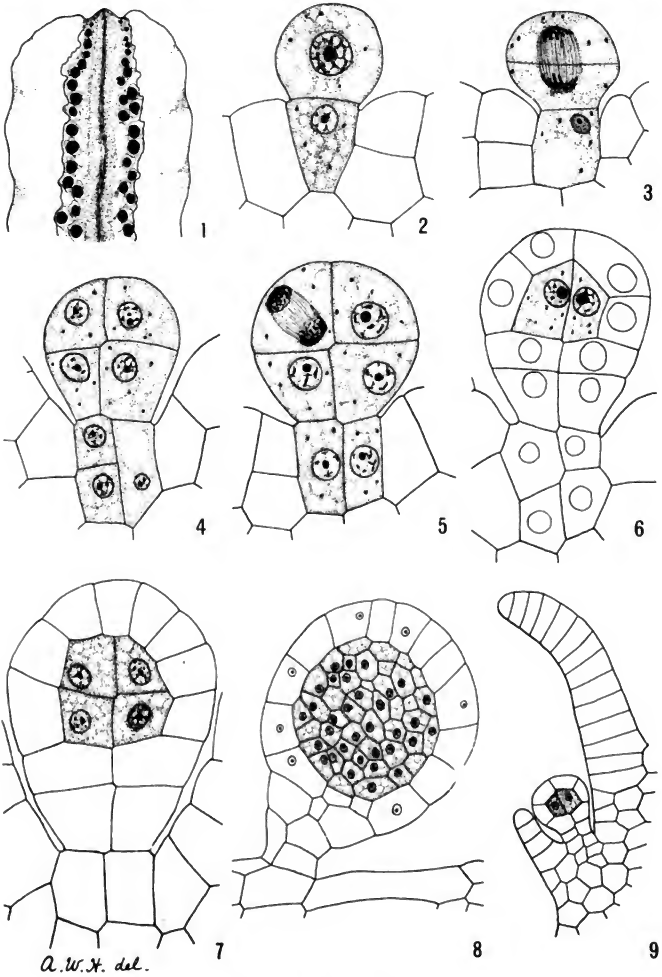
Fig. 29.—Older embryo showing haustorial cells and differentiation of sporogenous tissue; ×50; sketch of same stage; ×8.

Fig. 30.—Development of sporogenous tissue; ×50; sketch of same stage; ×8.

Fig. 31.—Sketch of older sporophyte; ×6.

Fig. 32.—Sporophyte containing mature spores and elaters; ×6.

Figs. 33–37.—Stages in development of spore mother cells; ×520.



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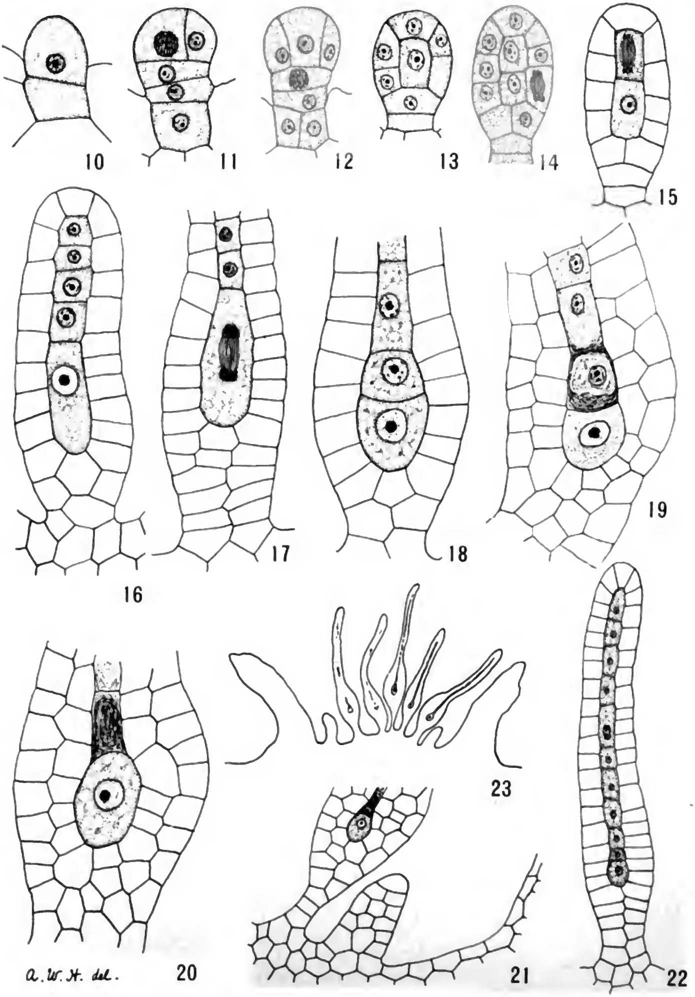

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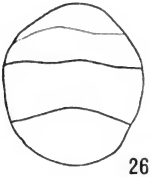
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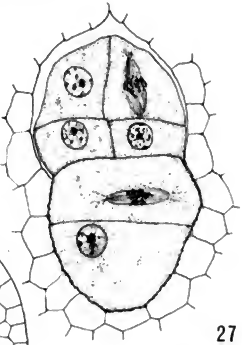
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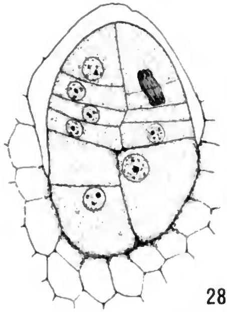
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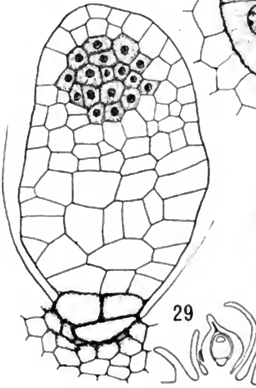
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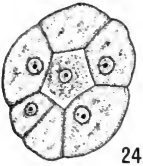
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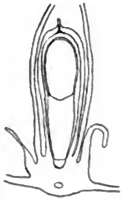
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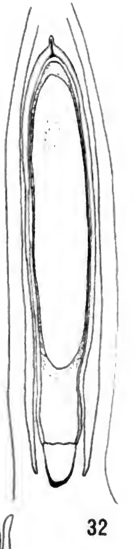
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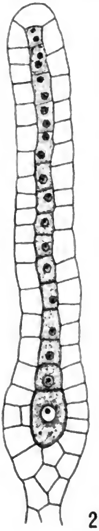
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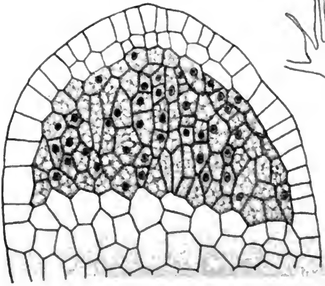
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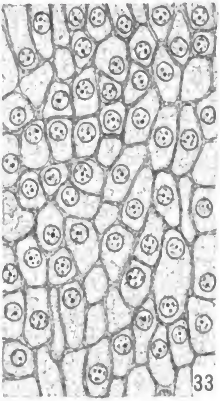
HAUPT on PALLAVICINIA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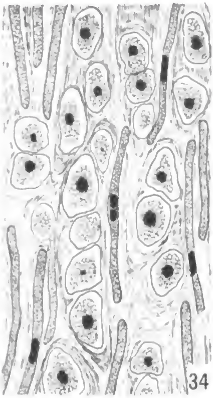
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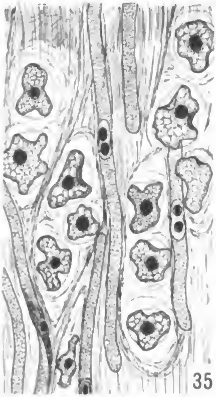
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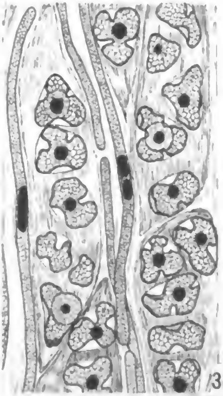
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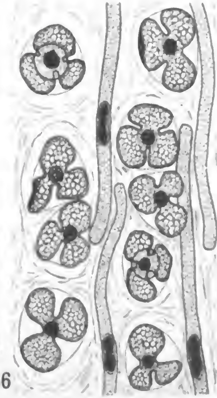
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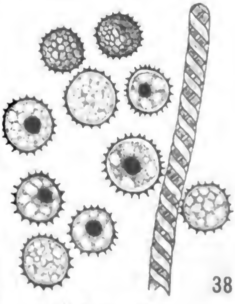
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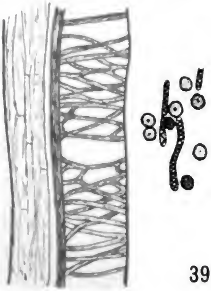
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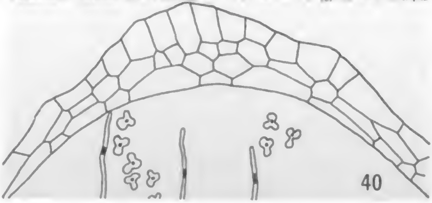
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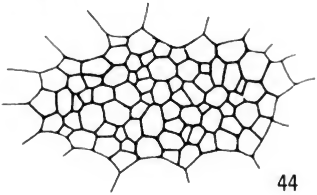
HAUPT on PALLAVICINIA



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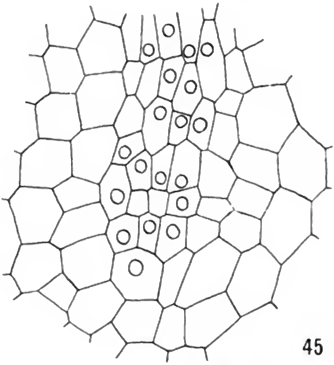

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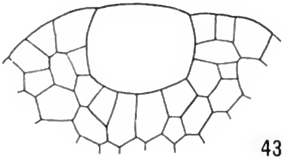

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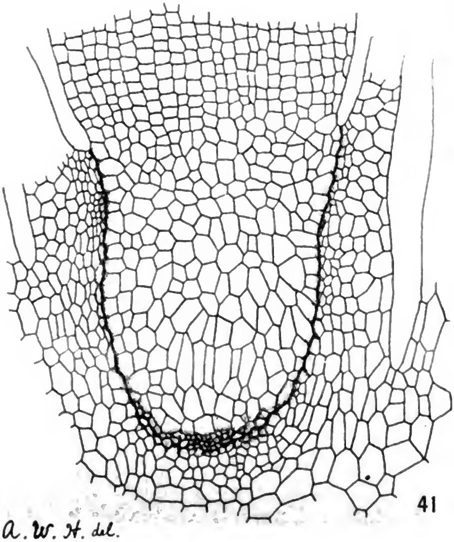

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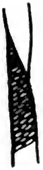

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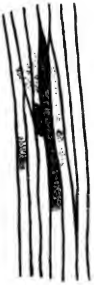

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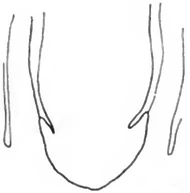

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A. W. H. del.

HAUPT on PALLAVICINIA

FIG. 38.—Mature spores and elater; ×630.

FIG. 39.—Wall of mature capsule and calyptra; ×30.

FIG. 40.—Median longitudinal section of sterile cap of capsule in mother cell stage; ×50.

FIG. 41.—Typical foot of mature sporophyte; ×30.

FIG. 42.—Anchor-like foot of sporophyte; ×15.

FIG. 43.—Median longitudinal section of apical cell; ×50.

FIG. 44.—Cross-section of cells in conducting strand; ×520.

FIG. 45.—Median longitudinal section of region directly back of apical cell showing differentiation of conducting cells; ×520.

FIG. 46.—Conducting cells showing pits; ×520.

FIG. 47.—Part of same; ×1040.

BRIEFER ARTICLES

MODIFICATION OF HAND MICROTOME

(WITH FIVE FIGURES)

Figs. 1–5 represent a simple modification of the familiar hand microtome, and one which has been found to be a decided improvement over the original instrument from which it was derived. In the ordinary type, when cutting sections of woody stems or more delicate material held in pith, it is always difficult to be certain of obtaining the necessary pressure for holding the material at the proper point. The steel rod which moves in or out upon the turning of the single pressure screw will usually hold the material firmly at its lower end but not so firmly at its upper end, with the result that the material has a tendency to wobble when the knife begins to cut the section. On the other hand, when this difficulty does not arise it is often almost impossible to screw up the material for the next section because of the pressure of the material against the walls of the tube or well.

To obviate these rather commonly encountered difficulties in the ordinary type of hand microtome the modification of it shown in the figures was devised. Figs. 4 and 5 give two views of an inner "material holder." It consists of two pieces of curved steel which are long enough to reach to the bottom of the tube or well (just below *cc* in fig. 2). This inner material holder is provided with a spreading spring at *ed* which surrounds a small steel bar *cc*. Each curved piece of steel has a hole at *aa* (fig. 4) through which project the ends of the two pressure screws *bb* (fig. 2). The manipulation of the apparatus is as follows where, for example, cross-sections of a woody stem are to be cut. The pressure screws *bb* are turned out until their ends at *aa* are pulled out of the holes in the material holder. The microtome is inverted and the material holder falls out. The stem or a portion of it is placed between the leaves of the material holder and properly oriented and, if necessary, a rubber band is bound around the material holder just above *aa*. The material holder containing the stem is now pushed down into the well or tube of the microtome and oriented so that the holes are opposite the ends *aa* of the turned-back pressure screws. These screws are turned in, their ends pass into the holes in the material holder, and pressure is finally exerted on both sides. As the pressure becomes

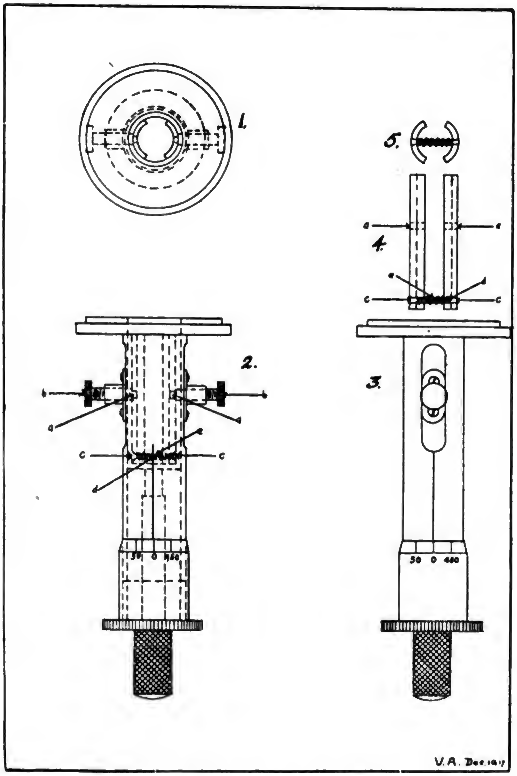

Fig. 1.—Modification of hand microtome

greater, the spring at *de* prevents the upper ends of the material holder from spreading and insures maximum pressure against the material at these upper ends. Finally the stem is held firmly in the center of the tube or well of the microtome between the leaves of the material holder. The pressure screws are free to move up or down in their openings because no appreciable pressure is exerted upon the walls of the tube or well.

In a similar manner material held in pith is very conveniently arranged in this apparatus. The possibility of arranging and orienting such material held in pith in the material holder outside the microtome is an obvious advantage. Longitudinal sections of small woody stems are readily cut in this modified hand microtome, whereas their small diameter makes it very difficult to secure them firmly in the original apparatus. As may be seen, it is possible to orient material to obtain all angles in the case of sections to be cut obliquely or in the case of unsymmetrical material.

This modified hand microtome was devised to meet a special need and has admirably served its original purpose. This description of it is presented primarily because it illustrates the possibility of modifying an apparatus in a relatively simple and inexpensive manner to increase greatly its convenience and the range of its usefulness. The original modification from which the drawing was made has been somewhat improved recently. The knurled heads *bb* should be much larger than those illustrated, and for woody stems the leaves of the material holder should be thicker and their inner surfaces more nearly flat.—T. H. GOODSPEED, *University of California.*

CURRENT LITERATURE

MINOR NOTICES

Fungous diseases and insect pests.—In a small volume issued as one of the Cambridge Farm Institute Series, PETHERBRIDGE[1] gives a popular account of the more common fungous diseases and insect pests of farm crops. The book is designed to be helpful to farmers and others who wish to acquire a knowledge of such things. The treatment is very elementary, but sufficiently extensive to give the uninitiated some idea of the nature of fungi and insects and their relation to agricultural crops. The text is nearly equally apportioned between the two main divisions of the subject-matter. The first division deals with fungi and fungous diseases, and the second with insect pests. Each division is introduced by a general chapter giving in each case a brief description of fungi, their mode of life, and the part they play in crop economy; and in the second part a general account of the structure, life histories, and habits of insects. In the special chapters the plan is followed of describing in detail some of the representative types of fungi and insects, as for instance, *Erysiphe graminis* as an example of the mildews, and grouping around them others of similar nature. An idea of the scope of the work can best be gained from the chapter headings, as follows: Introduction to fungi; Potato diseases and allied diseases; Finger and toe, and wart disease; Mildews; Ergot and clover sickness; Rusts; Smuts; Introduction to insects; Butterflies and moths; Beetles; Flies; Aphids and sawflies; Eelworms.

The book is written in a clear style and it will undoubtedly prove useful to the farmers of England in enabling them to identify the common insect and fungous diseases, and to find means of combating them. In the more extensive and diversified agriculture of the United States, where a vast special literature dealing with each particular condition is already available to the farmer, the book would find little application.—H. HASSELBRING.

Flora of the Northern Territory of Australia.—EWART and DAVIES[2] have published a flora of the large area known as the Northern Territory of Australia, not merely as a contribution to taxonomy, but also as an indication of "the fertility of the soil, the moisture conditions, and the fodder or other values of the natural vegetation." There are lists of plants of fodder value, valuable woods, poisonous and injurious plants, and medicinal plants. Four appendices also deal with Cyperaceae, Myrtaceae (except *Eucalyptus*), *Eucalyptus*, and *Acacia*. Four new genera are established by EWART as follows: *Spathia* and *Setosa* (Gramineae), *Rossittia* (Rutaceae), and *Carpentea* (Convolvulaceae); and in addition 30 new species are described.—J. M. C.

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[1] PETHERBRIDGE, F. R., Fungoid and insect pests of the farm. Cambridge. 1918.

[2] EWART, ALFRED J., and DAVIES, OLIVE B., The flora of the Northern Territory. 8vo. viii+387. *pls.* 27. Melbourne. 1917.

NOTES FOR STUDENTS

Phenomena of parasitism.—In a summary of his researches on the processes involved in the attacks of plant tissues by *Botrytis cinerea*, BROWN[3] gives a review of the work already published and a forecast of investigations now in progress. The published work has already been noted in this journal,[4] and we need only allude to the author's speculation on the question whether the effects produced by the fungous extract on the cell wall and on the protoplasm are attributable to the same or to different substances. In the absence of any means of disentangling the mixture of substances occurring in plant extracts or of excluding the action of all but one, it seems futile to speculate on the specificity of action of any of the substances. Future work as outlined by the author is to cover such problems as the germinating capacity of spores in water and in nutrient solutions, the diffusion of substances from plant cells into water placed on the cuticle, and the physics of cuticular resistance.

The fourth contribution to this series[5] deals with some of the factors influencing the production of cytase in cultures of *Botrytis cinerea*. In the first paper of the series it was shown that very active cytolytic extracts could be obtained from young germ tubes of the spores of the fungus. As might be expected, therefore, the activity of the enzyme extracted from cultures of different ages is proportional to the quantity of actively growing mycelium. Consequently, with respect to enzymatic activity, a growing culture soon reaches a maximum, and thereafter the enzyme content rapidly diminishes. The enzyme content of the culture fluid follows a course in general parallel to that of the mycelium. Dilution of the enzyme extract by a similar extract deactivated by exposure to a temperature of 65° has the same effect as dilution by distilled water. The lower enzyme content of old cultures, therefore, is not caused by the development of inhibiting substances. As might appear self-evident, cultures thickly sown with spores gave stronger enzyme extracts than cultures thinly sown. The experiments confirm the former conclusions that enzyme production is restricted to the growing ends of the hyphae.—H. HASSELBRING.

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[3] BROWN, W., On the physiology of parasitism. New Phytol. **16**:109–126. 1917.

[4] Rev. BOT. GAZ. **61**:80. 1916; **63**:240. 1917.

[5] BROWN, W., Studies in the physiology of parasitism. IV. On the distribution of cytase in cultures of *Botrytis cinerea*. Ann. Botany **31**:489–498. 1917.

Phytogeography of South Africa.—The very diverse vegetational types of South Africa have been classified and mapped by EVANS[6] in such a manner as to give a good idea of the ecological divisions of the southern part of that continent. The woodland has been subdivided into forest, scrub, bushveld, and palmveld. The first of these, which is mostly evergreen, is dominated by species of *Podocarpus*, while the scrub is a type of Sclerophyllous Shrub, in which the Proteaceae, Ericaceae, and Restionaceae contribute the dominant forms. From this the bushveld differs in its deciduous character and also in its more parklike aspect and its floristic composition. Bushveld is widely distributed, and while dominated by *Acacia* spp., such genera as *Tamarix*, *Combretum*, *Ficus*, *Zizyphus*, and *Rhus* are of common occurrence. The palm belt comprises a littoral strip on the southeast in which such palms as *Mimusops caffra*, *Phoenix reclinata*, *Raphia vinifera*, and *Cocos nucifera* mingle with succulents from the genera *Aloe* and *Euphorbia*.

The grassland covers the greater portion of the country with transitions to scrub and desert. That of the Kalahari region occupies much of the central portion of South Africa with an open formation, short, low, wiry grasses, species of *Aristida* and *Eragrostis*, occurring in isolated tufts. This and the other grasslands show transitions to the desert toward the west.

Four distinct desert types are briefly characterized and mapped, perhaps the most remarkable being the southern portion, a vast shallow basin, the Karroo, sparsely populated by succulent, tuberous, and bulbous plants. Prominent genera are *Crassula*, *Mesembryanthemum*, *Cotyledon*, *Euphorbia*, *Aloe*, *Stapelia*, *Senecio*, *Encephalartos*, and *Euclea*.

More important perhaps than the text, at least for the American botanist, are the excellent plates, enabling one to visualize the different types, and the map showing their distribution.—GEO. D. FULLER.

Pigment production in Penicillium.—BRENNER,[7] investigating the production of pigment in cultures of *Penicillium*, finds that in the absence of magnesium in the culture medium, or in the presence of ammonium salts whose utilization leads to an acid reaction of the culture fluid, no red, but only yellow pigment is produced. The red pigment is produced only in neutral media or in media developing an alkaline reaction. Iron apparently is not necessary for the formation of the red color. The author further reports a few preliminary experiments on the extraction and chemical reactions of the pigment which is insoluble in ether, chloroform, toluene, and similar organic solvents, but soluble in alcohol and dilute alkalies or ammonia. On account of the acid nature of the pigment the author attributes to it the physiological function of maintaining the neutrality of the medium.

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[6] EVANS, F. B. POLE, The plant geography of South Africa. Dept. Agric. Union of South Africa. Official Year Book. 1917. pp. 8. *pls. 24. map.* 1918.

[7] BRENNER, W., Die Farbstoffbildung bei *Penicillium purpurogenum*. Svensk. Bot. Tidskr. 12:91–102. 1918.

Many investigations have been made on the so-called influence of various environmental factors on the production of pigments by fungi, but a survey of the facts seems to indicate that between the absorption of an elementary nutrient and the production of a complex pigment two processes intervene to permit of the establishment of a direct relation between stages at the extreme ends of the series. A much better knowledge than is at hand at present of the nature and structure of fungous pigments is necessary before their physiological status can be determined. Different colors may often be due to the modification of the same pigment, depending on different reactions of the medium.—H. HASSELBRING.

Origin and goal of geobotany.—RÜBEL[8] has issued a compact and useful paper, dealing with the main phases of the development of geobotany and with the aims of its various subdivisions. Geobotany he regards as embracing all interrelations between plants and the earth, including much of ecology, chorology, chronology, and genetics; thus it includes all of phytogeography in the widest sense, and more. The historical presentation deals especially with the work of THEOPHRASTUS, TOURNEFORT, LINNAEUS, HALLER, SOULAVIE, WILLDENOW, HUMBOLDT, WAHLENBERG, and SCHOUW. Geobotany may be either floristic or vegetational, each of which subdivisions may consider the problems of space (distribution), habitat (ecology), or change (genetics). Thus RÜBEL recognizes 6 fields of geobotany: autochorology, or floristics; synchorology, or the distribution of plant associations; autecology, or the relation between the individual and the habitat; synecology, or the relation between the plant association and the habitat; autogenetics, or the change of floras; and syngenetics, or the change of plant associations. It appears to the reviewer that this is the most logical classification of these fields of study with which he is familiar. As a matter of practice, however, it is unlikely that investigators will increasingly recognize such subdivisions. A treatise dealing only with synchorology was fairly satisfactory in times gone by, but in these days it would seem sterile, except as livened up with ecology and genetics.—H. C. COWLES.

Continuous variation.—STOUT and BOAS,[9] as the result of their extensive statistical studies of variation in *Cichorium*, recommend that critical study of species variation should be based upon intensive studies of partial (existing among the parts of a single individual) and individual (characteristics of plants as wholes based on their entire record) variabilities. They suggest that failure to appreciate this necessity has allowed considerable error to creep into the work of a number of investigators. For example, hereditary studies of such characters as the size of flowers should be prefaced by an accurate knowledge of how such characters vary with relative place position on the plant or relative time position in the total period of bloom.

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[8] RÜBEL, EDUARD, Anfänge und Ziele der Geobotanik. Vierteljahrsschrift der naturforschenden Gesellschaft in Zürich **62**:629–650. 1917.

[9] STOUT, A. B., and BOAS, HELENE M., Statistical studies of flower number per head in *Cichorium Intybus:* kinds of variability, heredity, and effects of selection. Mem. Torr. Bot. Club **17**:334–458. *pls. 10–13.* 1918.

The authors have been able to isolate and maintain a number of races, but further state that "within each race there are further variations, continuous in gradation and of the same nature as those appearing in a more mixed population, which are unmistakable evidences of the instability of characters and hereditary units."—MERLE C. COULTER.

New-place effect.—COLLINS[10] has performed a rather unusual experiment with maize, testing the immediate effect of transferring various races to new habitats. We have abundant testimony that it is unwise to go very far from home for seed corn, and have generally concluded that local corn has become the best adapted to local conditions as the result mainly of artificial selection, whether conscious or unconscious. In accordance with this we should naturally suppose that to transfer seed would depress its yield (for a few generations at least). COLLINS, however, shows that while Texas seed of a given strain, planted side by side in Maryland with Maryland seed of the same strain, exceeds the latter in yield by 8 per cent; when the two are grown in Texas the Texas seed exceeds in yield the Maryland seed by only 2 per cent. It seems that the transfer of Maryland seed has acted as a stimulus to relatively greater yield. This phenomenon is termed "new-place" effect. It adds a further complication to the already perplexing problem of vigor in maize.—MERLE C. COULTER.

Dominance and parasitism.—JONES[11] finds support of his theory[12] that dominance accounts for hybrid vigor, from observations on susceptibility to parasitism in maize. It has hitherto been demonstrated by several investigators that resistance to parasitism behaves as a definite heritable factor. JONES shows that inbreeding corn serves to isolate certain homozygous races which are susceptible to smut and leaf blight while the more heterozygous ancestors are resistant. He concludes that "as in so many other cases, those factors which enable an organism to attain the best development tend to dominate." Thus, in general, the most heterozygous corn, which therefore shows the greatest hybrid vigor, will be the most resistant. A difficulty arises here, since certain diseases are known to thrive best in the most vigorous plants. It might be possible to account for this difference on the ground that certain diseases are immediately destructive to the host while others are not; although if this were true, JONES's leaf blight disease and smut should behave differently.—MERLE C. COULTER.

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[10] COLLINS, G. N., New-place effect in maize. Jour. Agric. Research **12**:231–243. 1918.

[11] JONES, DONALD F., Segregation of susceptibility to parasitism in maize. Amer. Jour. Bot. **5**:295–300. 1918.

[12] Rev. BOT. GAZ. **66**:70. 1918.

Lichen growth.—As the results of experiments and observations extending over a period of 8 years, FINK[13] has determined the rate of growth in certain crustose and foliose lichens, as determined by measurements of the diameter of the thallus, to vary from increases of 0.36 cm. per year for *Umbilicaria pustulata*, and 0.42 cm. for *Physica pulverulenta*, to 1.3 cm. per year for *Parmelia Borreri* and *P. caperata*, and 1.75 cm. for *Peltigera canina*. Some of the intermediate annual increments were 0.2–0.75 cm. for *Graphis scripta*, 0.6 cm. for *Verrucaria muralis*, and 1.16 cm. for *Parmelia conspersa*. In these measurements FINK has given us practically the only definite data we possess relative to the increase in size of these pioneer plants. With regard to migration, FINK declines to indulge in speculations regarding possible methods, and says "nothing is definitely known further than seeing parts of *Cladonia* thalli lying on some of the quadrats in early stages of ecesis."—GEO. D. FULLER.

Vegetation studies in Natal.—BEWS continues his interesting studies of the vegetation of Natal,[14] his latest paper dealing with the ecology of the Drakensberg.[15] These mountains exhibit picturesque and even stupendous scenery, the highest peaks being more than 11,000 ft. above the sea. The most extensive formation, as elsewhere in Natal, is the veld or grassland. The alpine veld is composed more of tussock grasses than is the lowland veld, and the growth forms are more xerophytic. An interesting formation is the *Protea* veld, dominated by various species of small trees of the genus *Protea*. The climax formation is the bush, dominated by species of *Podocarpus*, and occupying the more protected situations. The mountain top vegetation is markedly xerophytic, and is dominated by composites (as *Helichrysum*) and heathers (as *Erica*). The last section of the paper deals with successions and interrelations.—H. C. COWLES.

Tree growth in Iowa.—In presenting data upon tree growth in the vicinity of Grinnell, Iowa, CONARD[16] brings out several interesting facts in addition to the average annual increment of several species. There seems to be conclusive evidence that trees are encroaching upon the grasslands, and this is ascribed to the elimination of prairie fires during the past half century. While this accounts for the present increase of forested areas, it is not regarded as explaining the presence of grasslands which constituted the natural vegetation upon the best soils in the region. These richer soils are very favorable to tree growth and the increments are sufficiently large to indicate that timber would prove a profitable crop. Some typical average annual increments are *Carya ovata* 0.22 inch, *Quercus macrocarpa* 0.30 inch, *Q. velutina* 0.29 inch, *Acer saccharinum* 0.63 inch, and *Juglans nigra* 0.34 inch.—GEO. D. FULLER.

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[13] FINK, BRUCE, The rate of growth and ecesis in lichens. Mycologia **9**:138–158. 1917.

[14] BOT. GAZ. **64**:85–86. 1917.

[15] BEWS, J. W., The plant ecology of the Drakensberg Range. Annals Natal Museum **3**:511–565. *pls. 4. figs. 3.* 1917.

[16] CONARD, H. S., Tree growth in the vicinity of Grinnell, Iowa. Jour. Forestry **16**:100–106. 1918.

Inheritance of height in peas.—According to MENDEL's original classic experiment with peas, the cross tall×dwarf gives a simple monohybrid ratio, with tallness dominant. The work of a number of recent investigators, however, has indicated that height in peas is a much more complex character, and that Mendel's 3:1 ratio by no means states the whole truth. WHITE[17] has made a critical examination of these investigations and has added some of his own. He concludes that there are at least 5 genetic factors involved, 2 for internode length, and 3 for number of nodes. He points out, however, that the same genetic pea material that MENDEL used will still give the 3:1 ratio. "The inheritance of height in peas has become complex only because of studies on new or distinctly different material, the characters of which, there is reason to believe, are due to distinct mutations."—MERLE C. COULTER.

Intercellular canals.—RECORD[18] has investigated the occurrence of intercellular canals in dicotyledonous woods, and has discovered 16 families in which they occur, mostly tropical. In some cases they are a normal feature of the wood, while in other cases they develop as a result of injury. They vary in direction and origin, in certain features resembling those of gymnosperms, but in many important features quite distinct. The secretions exhibit a wide range of variation, being resinous, oily, gummy, or tanniferous, as contrasted with conifers, in which the secretions are wholly resinous. RECORD concludes that the presence of intercellular canals in wood is a valuable diagnostic feature, and it was with this primarily in view that the investigation was made.—J. M. C.

Inheritance in Pisum.—WHITE[19] has presented a very significant paper on the interrelation of the genetic factors of *Pisum*. He has collected a mass of data of his own and also of earlier investigators of *Pisum*. He distinguishes 35 factors and discusses 5 linkage groups. A model section appears under the title "Modification of the expression of *Pisum* factors by different environments and by each other." This is one of the first successful attempts to make an intensive study of inheritance in plants, such as has been so well made on the fruit fly. Another such study, on corn, is now maturing at Cornell under the direction of Dr. R. A. EMERSON.—MERLE C. COULTER.

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[17] WHITE, ORLAND E., Inheritance studies in *Pisum*. III. The inheritance of height in peas. Mem. Torr. Bot. Club **17**:316–322. *fig. 1.* 1918.

[18] RECORD, S. J., Intercellular canals in dicotyledonous woods. Jour. Forestry **22**:429–441. 1918.

[19] WHITE, ORLAND E., Inheritance studies in *Pisum*. IV. Interrelation of the genetic factors of *Pisum*. Jour. Agric. Research **11**:167–190. 1917.

Rusts of Oregon.—JACKSON[20] has published an annotated list of the rusts of Oregon, which brings together for the first time the rust flora of a state on the Pacific coast. All of the grain rusts recorded for North America (except *Puccinia Sorghi*) are known to occur in the state, and also all of the rusts of greenhouse crops. In addition to these, the Pacific coast rust of pears and quinces is said to be of considerable economic importance; and of course the forest-tree rusts represent an important field of investigation. The list includes 220 species of rusts occurring on about 500 different hosts, 8 of the species being described as new.—J. M. C.

Practical breeding.—COLLINS and KEMPTON[21] have given an excellent example of the effective application of the principles of pure science to the solution of a practical problem. The production of a race of sweet corn resistant to the earworm has been a strictly practical problem, and introduces no new phenomena or theories of inheritance. The authors, however, have established statistically the correlation between the amount of damage done by the earworm and certain superficial plant characters, and have followed this by selective breeding for those significant characters.—MERLE C. COULTER.

The morning glory in genetics.—BARKER[22] has found that the morning-glory is very favorable material for work in genetics. The almost innumerable combinations of floral colors are beautifully explained by the enzyme theory. "Each epistatic type is due to the addition of one or more genes, probably enzymatic in nature, which are not present in the hypostatic type."—MERLE C. COULTER.

Rusts of Cuba.—ARTHUR and JOHNSTON[23] have brought together all collections of Cuban rusts as a "basis for a thoroughly scientific and economic exploration of the island." The list includes 140 species, 12 of which are described as new, 15 are new to the North American flora, and 10 are exclusively Cuban.—J. M. C.

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[20] JACKSON, H. S., The Uredinales of Oregon. Mem. Brooklyn Bot. Gard. **1**:198–297. 1918.

[21] COLLINS, G. N., and KEMPTON, J. H., Breeding sweet corn resistant to the corn earworm. Jour. Agric. Research **12**:549–572. 1917.

[22] BARKER, E. E., Hereditary studies in the morning-glory (*Ipomaea purpurea*). Cornell Univ. Agric. Exper. Sta. Bull. no. 392. pp. 38. *pls. 3.* 1917.

[23] ARTHUR, J. C., and JOHNSTON, J. R., Uredinales of Cuba. Mem. Torr. Bot. Club **17**:97–175. 1918.

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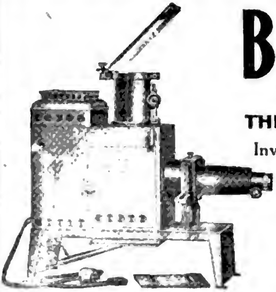

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